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Mountain Pine Beetle Dynamics in Lodgepole Pine Forests

Part I: Course of an Infestation

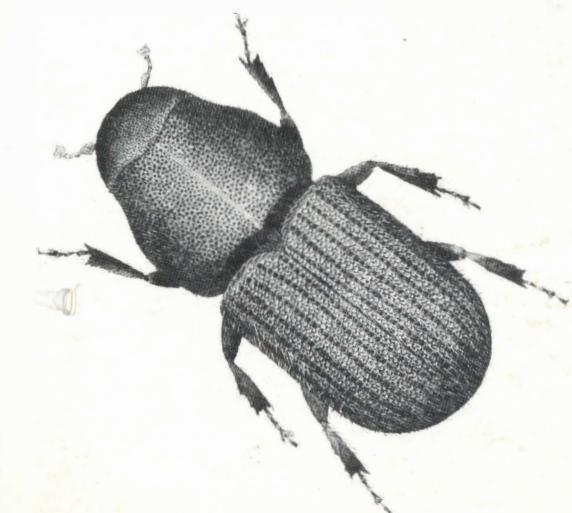
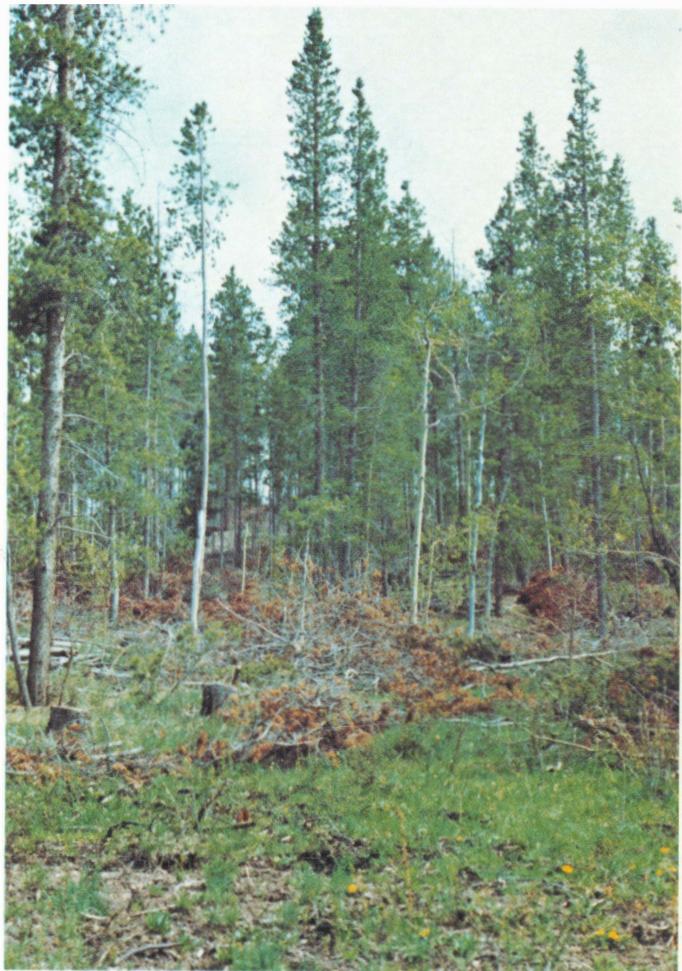
Walter E. Cole and Gene D. Amman



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THE AUTHORS

WALTER E. COLE is Project Leader of the Population Dynamics of the Mountain Pine Beetle research work unit in Ogden, Utah. This unit was started in 1960 under his direction, as was the early research groundwork on the mountain pine beetle. Prior to this assignment, he did population dynamics research, control, and survey work on the spruce budworm and pine butterfly in southern Idaho. He did biological research and survey data collection on the spruce bark beetle in Fort Collins, Colo. He began his career with Forest Insect Investigations, Bureau of Entomology and Plant Quarantine, as supervisory control and survey aid in Berkeley, Calif. Dr. Cole has authored 31 publications.

GENE D. AMMAN is Principal Entomologist on the Population Dynamics of the Mountain Pine Beetle research work unit in Ogden, Utah, an assignment that began in 1966. He has contributed a major portion of the biological and a substantial amount of the management research on the mountain pine beetle. Prior to joining the Intermountain Station, he was research entomologist with the Southeastern Forest Experiment Station in Asheville, N.C., doing biological control and ecological research on the balsam woolly aphid. He began his career with the Rocky Mountain Experiment Station in Fort Collins, Colo., as research assistant on sampling populations and mortality factors of the spruce bark beetle. He has authored 45 publications.

COVER PHOTOS:

Bottom left photo: Typical expanses of beetle-killed lodgepole pine.

Top right photo: Cutting strategies developed to prevent beetle kills--5 years after--still no beetle kill.

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MOUNTAIN PINE BEETLE DYNAMICS IN LODGEPOLE PINE FORESTS

PART I: COURSE OF AN INFESTATION

Walter E. Cole and Gene D. Amman

INTERMOUNTAIN FOREST AND RANGE EXPERIMENT STATION
U.S. Department of Agriculture
Forest Service
Ogden, Utah 84401

PREFACE

The mountain pine beetle, *Dendrotonus ponderosae* Hopkins, is a native bark beetle whose depredations cause various effects upon the lodgepole pine, *Pinus contorta* Douglas, var. *latifolia* Engelmann, ecosystem. Historically, the beetle kills millions of trees each year in the United States and Canada. During epidemics, a single National Forest may lose in excess of a million trees in a single year; for example, 3.6 million lodgepole pines were killed on the Targhee National Forest, Idaho, in 1976 (Klein and others 1979). The mountain pine beetle has killed an estimated average of two billion board feet per year since 1895 (Wood 1963). In 1970, volume loss of growing stock to all mortality causes totaled some 613 million ft³ (17.4 million m³) within the Rocky Mountain States; this is equivalent to nearly 75 percent of the volume that went into roundwood products. Sawtimber volume losses approximated 208 million ft³ (5.9 million m³) equivalent to almost 50 percent of the roundwood products output from sawtimber (Green and Setzer 1974). The mountain pine beetle in lodgepole and ponderosa pines accounted for about 473.3 million ft³ (13.4 million m³) or 77 percent of this timber loss. Similar losses could be expected in the West Coast States. In western Canada, losses of lodgepole pine to the mountain pine beetle were estimated to be 1.3 million ft³ (36 900 m³) per year between 1950 and 1970 (Safranyik and others 1975). This impact places the mountain pine beetle as the prime insect agent affecting the lodgepole pine ecosystem. The effects of beetle infestations change the entire lodgepole pine environment, and, depending on subsequent occurrence or exclusion of fire, largely determine the nature of successional dynamics--to lodgepole pine renewal in the case of fire, or to succession of more shade-tolerant species in the absence of fire.

Tree mortality in pine stands can occur as scattered individual trees, but more often entire groups of trees are killed. Unchecked, these groups expand with succeeding beetle generations, and eventually large areas may suffer extreme losses of their forest cover. This may or may not be a catastrophic situation, depending on landowner objectives. Some landowners, for example, favor grassland over timberland and a bark beetle outbreak may in fact be no disaster in their eyes. On the other hand, the value of a mountain home may be severely reduced by the death of high-value shade trees and the owner may view this loss as highly undesirable. From the timber-producer standpoint, the beetle can disrupt management plans and cause an unwelcomed impact on local, regional, and national economies.

This treatise represents much original research by the authors, but also is a review of other published literature about the mountain pine beetle, with particular reference to epidemic infestations. Much research remains to be done in testing and applying management strategies indicated by this research. In addition, the dynamics of mountain pine beetle populations during endemic periods are in need of study. During periods of low beetle activity, we believe significant "keys" exist that will permit more effective management of stands to prevent increases in beetle populations.

Our research approach first addressed the recognition and determination of relationships between the insect and its associated environmental factors. These relationships were based on biological functions and they were studied to determine their biological effect upon the insect. Secondly, quantification of these relationships was based upon measurement units relative to beetle behavior. The host variable was considered as an integral unit within the ecosystem.

It is our intent to lead the reader through this maze of interactive relationships to the extent of his interest and existing knowledge on the subject. With this in mind, we have prepared three sections:

- I. Course of Infestation--including beetle impact on the lodgepole pine stand, how the beetle "moves through" the stand, expected timber mortality, and management alternatives.
- II. Mountain Pine Beetle Population Dynamics--including bionomics, analyses of mortality factors, entomological relationships, and the "inner workings" of a mountain pine beetle population.
- III. Modeling of the Mountain Pine Beetle Populations within a Stand of Lodgepole Pine--including display and progression of all variables studied within both beetle and tree populations.

RESEARCH SUMMARY

Much of this work is original research by the authors. However, published literature on the mountain pine beetle is reviewed with particular reference to epidemic infestations in lodgepole pine forests. The mountain pine beetle and lodgepole pine have evolved into an intensive and highly compatible relationship. Consequently, stand dynamics of lodgepole pine is a primary factor in the development of beetle epidemics. The diameter-growth relationship and the effects of environmental factors on the beetle population provide the basis for assessing potential tree losses and some forest management alternatives to be used. Stand susceptibility and acceptable risks are considered in the use of these management alternatives in order to achieve management's goals.

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THE HOST

Lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann) forests provide important cover on more than 13 million acres (5.2 million ha) in 11 western States (Wellner 1975) and over 49.5 million acres (19.8 million/ha) in western Canada (McDougal 1975). These forests serve many purposes, such as cover on scenic backdrops for recreational areas, protective cover on watersheds, habitat for game animals, grazing for domestic livestock, and raw materials for lumber, poles, posts, and pulp (Tackle 1954). Lodgepole pine has a wide geographic range extending from Alaska south to northern Baja California and east through Wyoming and Colorado. Elevationally, it can be found from sea level in Alaska to 11,500 feet (3 485 m) in Colorado, with best development occurring where the annual precipitation is 21 inches (53 cm) or more (Mason 1915). Lodgepole pine has considerable commercial importance in Utah, Oregon, Montana, Idaho, Wyoming, and Colorado; more than 80 percent of the lodgepole pine in the United States occurs in the last four States (Wikstrom 1957).

Ecologically, lodgepole is typically described as seral, with low shade tolerance; as possessing the ability to grow on almost any forest site; as having both open and serotinous cones (serotinous cones require high temperatures to open and release seed); as regenerating rapidly in large numbers that create stagnated stands; as having rapid growth in young trees and slow growth in old trees; and as having high susceptibility to mistletoe infection and premature mortality from mountain pine beetle attack (Pfister and Daubenmire 1975). Many of these characteristics contribute to large fuel buildups that lead to intense fires over large areas, thus renewing the lodgepole pine cycle (Brown 1975).

Pfister and Daubenmire (1975) recognized four basic successional roles for lodgepole pine:

1. *Minor seral.*--Lodgepole pine is a minor component of young, even-aged, mixed species stands. It is rapidly replaced by shade-tolerant associates in from 50 to 200 years; the more mesic the site, the sooner lodgepole pine is replaced.

2. *Dominant seral.*--Lodgepole pine is the dominant cover type of even-aged stands with a vigorous understory of shade-tolerant species that will replace the lodgepole in from 100-200 years. Succession occurs most rapidly where lodgepole pine and shade-tolerant associates become established simultaneously. Lodgepole pine gains dominance through rapid early growth, but shade-tolerant species persist and assume dominance as individual lodgepole pines die.

3. *Persistent.*--Lodgepole pine forms the dominant cover type of even-aged stands with little evidence of replacement by shade-tolerant species. These species are present only as scattered individuals, but apparently are too few and lack sufficient vigor to replace lodgepole pine. Lodgepole pine maintains its dominance because of inadequate seed sources from potential competitors, stand densities too great to allow regeneration of any other species, and light surface fires that remove seedlings without killing overstory lodgepole pine.

4. *Climax.*--Lodgepole pine is the only species capable of growing on particular sites and is self-perpetuating. Some examples: In central Oregon, lodgepole pine forms an edaphic climax on poorly drained soils and a topoedaphic climax in frost pockets (Franklin and Dyrness 1973). In Wyoming, lodgepole forms an edaphic climax on granitic soils in portions of the Bighorn Mountains (Despain 1973) and on shallow, infertile soils of schist origin in portions of the Wind River Mountains (Reed 1976). Lodgepole pine also forms an edaphic climax on obsidian sands in the West Yellowstone area of Montana (Pfister and others 1977).

The occurrence of lodgepole as a seral type is largely due to fire, which eliminates competing climax vegetation, thus leaving the site open to colonization by lodgepole pine. Cones in many lodgepole stands are predominantly of the closed type, thus assuring a large supply of seed for colonization of the site after a fire (Lotan 1967). Fire, however, is not a requisite for seed release from closed cones; cones can open when enough heat from insolation reaches the cones to melt the resin that seals the scales (Clements 1910).

Lodgepole pine frequently regenerates too abundantly, resulting in overstocking and stagnation at an early age. Many stands are so stagnated that at age 70 they may contain 100,000 trees/acre (247 000/ha) and average 40 feet (12 m) in height and less than 10 inches (25 cm) in diameter at ground level (Mason 1915). Consequently, great range exists in stand density and board foot volume in lodgepole pine stands. Tackle (1961) gave an example of two stands to illustrate this range: A 100-year-old stand yielded 20,000 bd.ft. per acre (49,400 bd.ft./ha) with 800 trees per acre (1 976/ha); in contrast to a second stand that yielded only 1,500 bd.ft. when the number of trees was 1,800 per acre (4 448/ha). Once stagnation occurs, adequate growth rates may be difficult to renew (Tackle 1959).

THE EPIDEMIC FORM

The mountain pine beetle infests extensive areas of lodgepole pine and probably has been active in the ecosystem almost as long as there have been lodgepole pine trees. Evidence of several early outbreaks, including one that was active in the Horse Creek territory of Utah more than 180 years ago, was discovered by Thorne (1935).

A small mountain pine beetle outbreak beginning in 1909 was reported on the Flathead National Forest in the Northern Rockies¹. During a succeeding 25 to 30 years, new infestations appeared throughout much of the Rocky Mountains and increased to epidemic levels on the National Forests and National Parks as far south as the Cache National Forest in Utah. These infestations were reduced considerably, particularly on the northern forests, when extremely low temperatures in December 1932 and again in February 1933 caused high mortality of overwintering broods.

One of the most obvious effects of tree killing by mountain pine beetles where lodgepole pine is seral is the depletion of lodgepole pine and the hastening of succession by climax species (Roe and Amman 1970). Frequency of infestations on a given area of forest appears to range from 20 to 40 years, depending upon stand location and on how rapidly the stand grows into conditions conducive to buildup of beetle populations (trees of large diameter and thick phloem at low to middle elevations) (Roe and Amman 1970; Amman and Baker 1972).

Where fire has been absent for 100 years or more, examination of surviving trees within stands reveals periods of mountain pine beetle activity and successional trends. In such examinations, an upward trend in growth curves reflects release of the understory following death of lodgepole pine in the overstory. For example, in a stand in the Dell Creek drainage, Teton National Forest, Wyoming (fig. 1), the rather abrupt increase in growth from 1907 to 1927 reflects mountain pine beetle-caused release during that time. In this stand, where lodgepole pine has become only a minor component, not all trees in the stand showed simultaneous release as would be expected from weather effects. Furthermore, available weather records from the nearest, but somewhat distant, stations showed generally below average precipitation between 1917 and 1937.

¹Evenden, James C. 1934. History of the mountain pine beetle infestation in the lodgepole pine stands of Montana. Unpubl. rep. 25 p. USDA For. Insect Lab., Coeur d'Alene, Idaho.

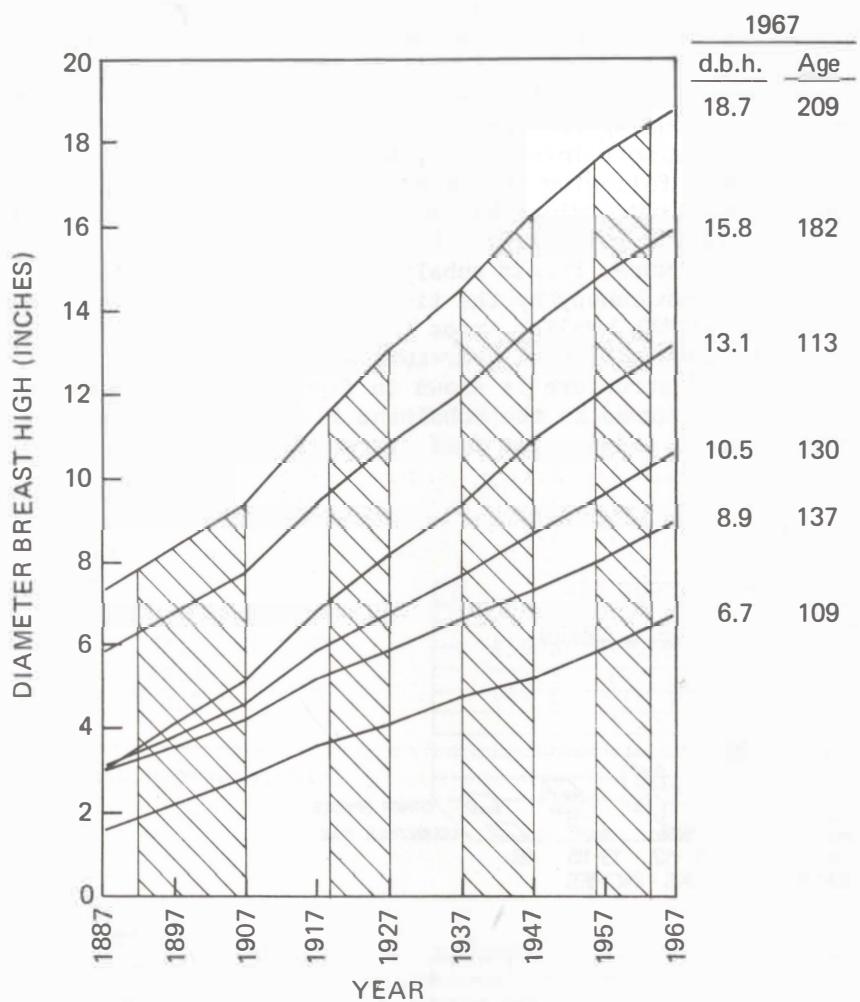


Figure 1.--Diameter trend curves of residual subalpine fir trees during four mountain pine beetle infestations in the lodgepole pine overwood, Dell Creek, Teton National Forest. The superimposed crosshatched bars show the periods of infestation (Roe and Amman 1970).

The greatest release of subalpine fir in the Dell Creek stand followed the first suspected infestation that took place from 1892 to 1907. During that period, 95 percent of the cores showed significant release and this is reflected in the upward trend of diameters following 1907. This trend continued for two decades into the middle of a moisture deficient period, 1917 to 1937, as well as through a second infestation. During a third infestation, from 1937 to 1947, the diameter curves steepened again, probably reflecting release during that period. Whereas larger trees showed the greatest release effect during the earliest infestation, the three smallest classes of trees displayed continued response following the later infestations. Greater number of lodgepole pine trees were killed during the earlier infestations than during the later ones; consequently, the earlier infestations had a greater release effect upon the subalpine fir stand. Furthermore, larger subalpine fir trees had attained a more dominant position in the crown canopy by the time of the last infestation; so they were not as subject to release as the smaller trees. The curves illustrate development of the fir understory as the lodgepole pine overstory was reduced by repeated beetle infestations. Present stand structure is shown in figure 2. Some mortality from undetermined factors also occurred in the subalpine fir stand as reflected by the 17 ft² (1.5 m²) of basal area recorded under dead trees (table 1).

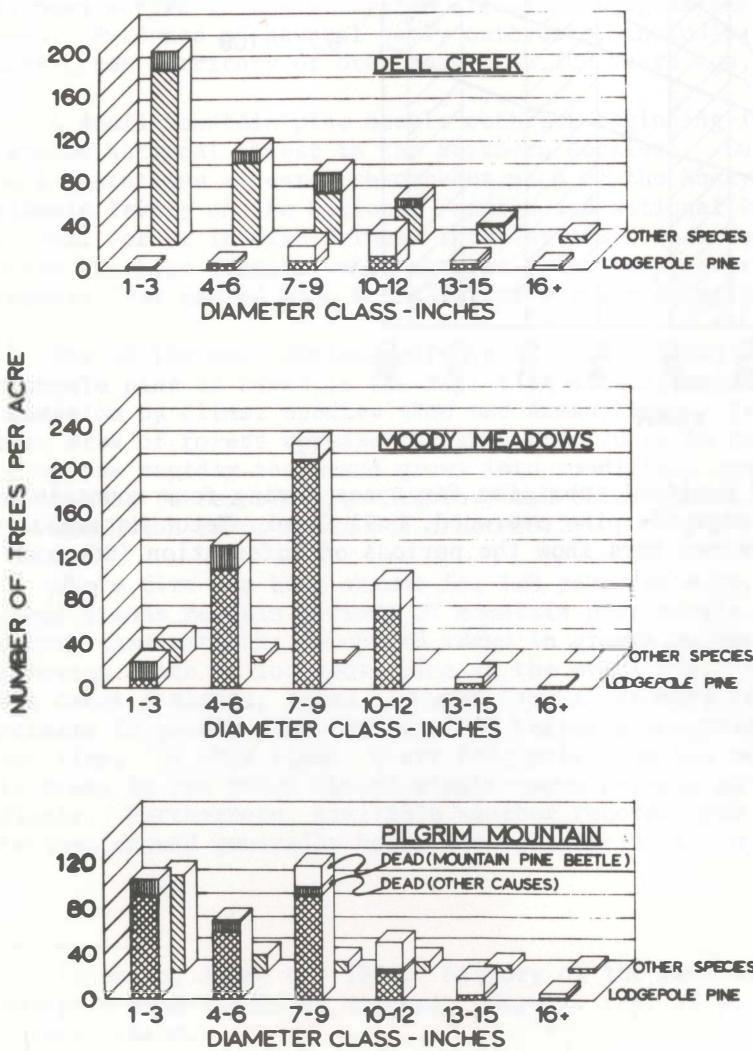


Figure 2.--The distribution of postepidemic live and dead trees on Dell Creek and Pilgrim Mountain areas, Teton National Forest, and the Moody Meadows area, Targhee National Forest (Roe and Amman 1970).

Table 1.--Basal area summarized for three areas examined that have sustained one or more mountain pine beetle infestations (Roe and Amman 1970)

Tree condition	Dell Creek	Moody Meadows	Pilgrim Mountain
----- Ft ² (m ²) -----			
Lodgepole pine			
Live	14.9 (1.3)	137.8 (12.4)	66.5 (6.0)
Dead ¹	27.5 (2.5)	28.8 (2.6)	46.8 (4.2)
Dead ²	-- --	5.6 (0.5)	6.2 (0.6)
Total	42.4 (3.8)	172.1 (15.5)	119.5 (10.8)
Subalpine fir and other species			
Live	73.8 (6.6)	1.7 (0.2)	26.5 (2.4)
Dead ²	17.0 (1.5)	-- --	-- --
Total	90.8 (8.2)	1.7 (0.2)	26.5 (2.4)
All species			
Live	88.7 (8.0)	139.5 (12.6)	93.0 (8.4)
Dead	44.5 (4.0)	34.3 (3.1)	53.0 (4.8)
Total	133.2 (12.0)	173.8 (15.7)	146.0 (13.2)

¹Killed by mountain pine beetle.

²Other causes.

Examination of another stand in which lodgepole pine was predominant near Moody Meadows on the Rexburg District, Targhee National Forest, Idaho, revealed two infestations (Roe and Amman 1970). The first infestation occurred between 1937 and 1947 (fig. 3). Some control effort (felling and spraying infested trees) was applied in the stand in 1946. This first infestation was light and probably was checked by the control effort or the beetles were unable to sustain themselves in the thin-barked trees in the stand. The same stand was infested 21 years later (1967) by a more intensive infestation--46.9 trees per acre (115.8/ha) were killed as contrasted with 17.7 trees per acre (43.7/ha) in the first infestation. Surviving trees after the last infestation ranged between 4 and 16 inches diameter breast height (d.b.h.) (10.2 to 40.6 cm) and from 54 to 106 years old with a mean age of 87 years. The Moody Meadows stand is stocked with 516 trees per acre (1 275/ha), 1 inch d.b.h. (2.5 cm) and larger, and these are distributed among diameter classes as shown in figure 2.

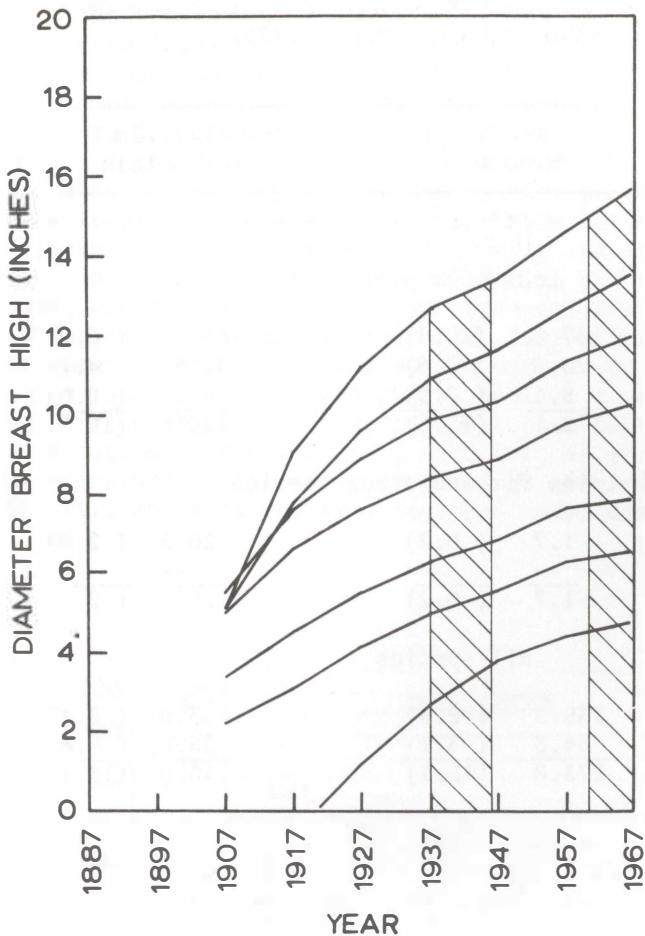


Figure 3.--Diameter trend curves of residual lodgepole pine trees in the Moody Meadows area, Targhee National Forest. The two periods of beetle infestation are shown by superimposed crosshatched bars (Roe and Amman 1970).

Residual lodgepole pine trees in the Moody Meadows stand show definite release as illustrated by the upward trend in diameter following the 1937 to 1947 infestation (fig 3). The release effect appears to be most pronounced in the larger trees, particularly those located in or near the margin of openings created by the earlier infestation. The released trees have continued to grow well to the present time, but trees in other parts of the stand show signs of growth reduction for several years prior to 1967. Significant release is not yet apparent from the thinning caused by the current infestation; further growth of residual trees, however, can be expected to provide suitable trees for future infestations.

A subalpine fir understory in the Moody Meadows stand of about 29 trees per acre (72/ha) averaged 2.6 inches (6.7 cm) in diameter and ranged from 1 to 7 inches (2.5 to 17.8 cm). In addition, 1,115 subalpine fir seedlings, 3 inches (7.6 cm) tall to 1 inch (2.5 cm) d.b.h., occurred per acre (2 754/ha). These will fill openings in the overstory as they are created by future beetle infestations (fig. 2).

In 1967, a third stand of lodgepole pine on Pilgrim Mountain in the northwestern part of the Teton National Forest bordering Teton National Park was undergoing its first known infestation of mountain pine beetles. The stand contained 492 trees per acre (1 215/ha) that were 1 inch (2.5 cm) d.b.h. and larger. The age of the residual trees 4 inches (10.2 cm) d.b.h. and larger ranged from 33 years to 113 years with a mean age of 76 years. The distribution of trees by diameter groups is shown in figure 2 and stand basal areas are shown in table 1. No well-defined release effect was evident in the diameter trends for the Pilgram Mountain stand, and diameters showed a steady increase through the life of the stand.

These observations suggest that the mountain pine beetle, by periodically removing the largest lodgepole trees from the stands, has been instrumental in hastening succession of lodgepole pine by climax species (Roe and Amman 1970). In addition, the mountain pine beetle plays an important role in changing even-aged to uneven-aged stands in the absence of fire, particularly where lodgepole pine is persistent or climax.

Lodgepole pine is persistent over large acreages and because of a small number of shade-tolerant individuals of other species found in such stands, the successional status is unclear (Pfister and Daubenmire 1975). In any case, lodgepole pine persists long enough for a number of beetle infestations to occur. In such cases and in those cases of a more limited nature that occur because of special climatic or edaphic conditions when lodgepole pine is climax, the forest consists of trees of different sizes and ages ranging from seedlings to a few overmature individuals. In these forests, the beetle infests and kills most of the lodgepole pines as they grow to larger sizes. Openings created in the stand as a result of the largest trees being killed are seeded by lodgepole pine (fig. 4). The cycle is then repeated as other lodgepole pines reach sizes and phloem thicknesses conducive to increases in beetle populations.

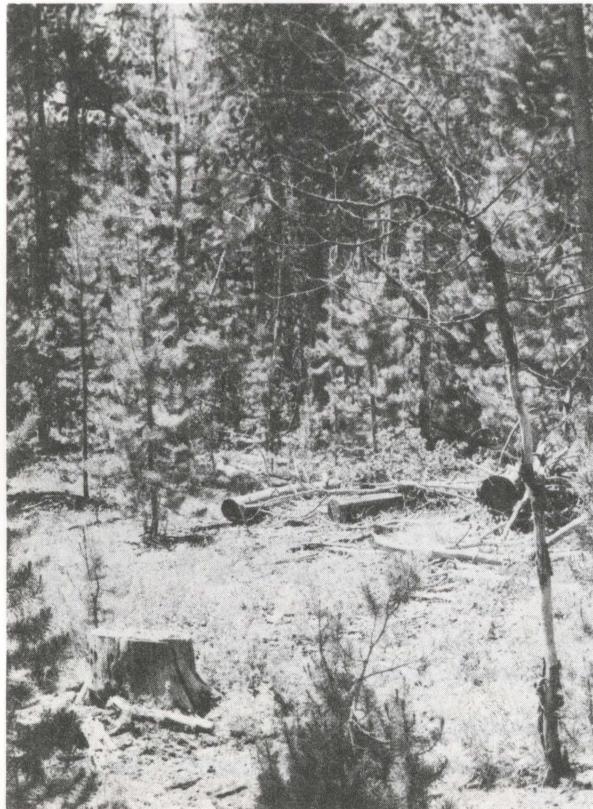


Figure 4.--Openings created when the mountain pine beetle kills large dominant trees in persistent and climax lodgepole pine stands are seeded by lodgepole pine. Stump is remnant of tree killed by mountain pine beetle about 12 years previously.

The result is two- or three-story stands consisting of trees of different ages and sizes (Roe and Amman 1970). A mosaic of small clumps of different ages and sizes may occur. The overall effect is likely to result in more infestations by the beetle because of the more constant source of food. Beetle infestations in such forests may kill fewer trees per acre during each infestation than would occur in even-aged stands developed after fires and in those where lodgepole pine is seral (Amman 1977).

A typical diameter distribution within a green stand in which a mountain pine beetle epidemic might occur is shown in figure 5. A relatively large proportion (22 percent) of the stand (trees more than 4 inches [10.2 cm] d.b.h.) is in trees more than 12 inches (30.5 cm) d.b.h.--a condition regarded as conducive for an epidemic (Cole and Amman 1969; Amman 1969).

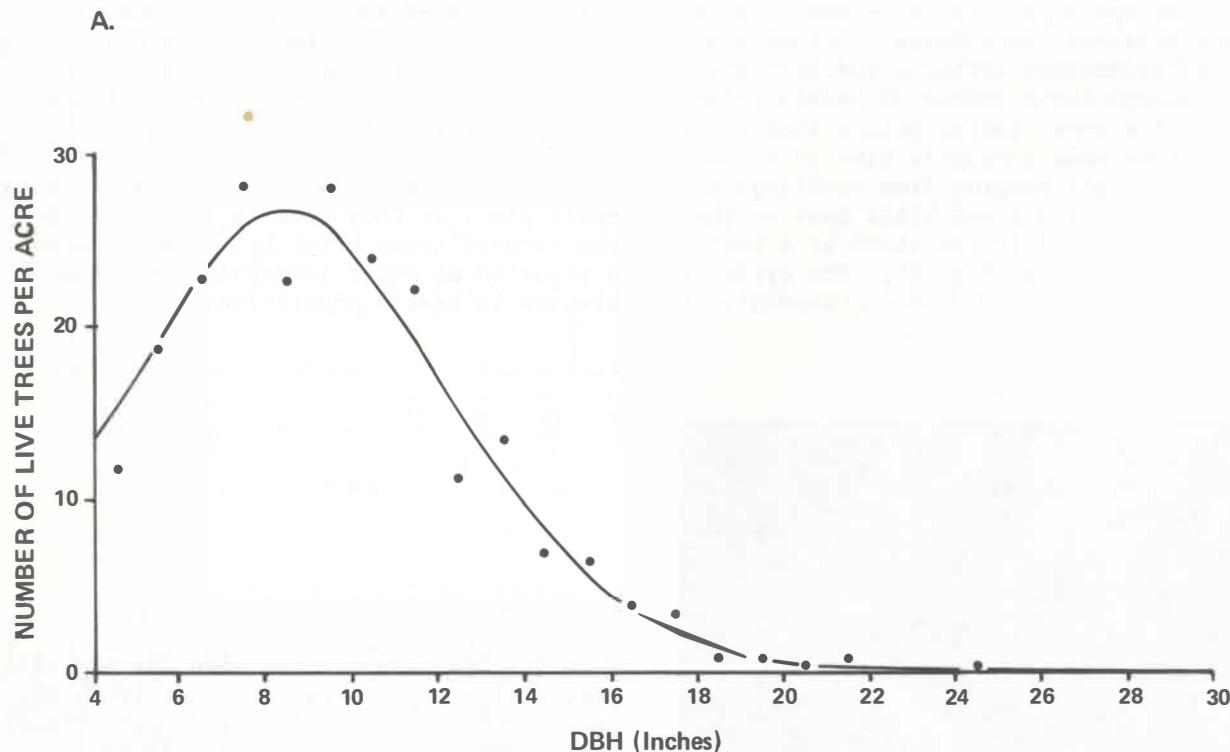


Figure 5.--Green stand structure at the beginning of a mountain pine beetle infestation (Cole and others 1976).

A generally accepted graphical description of the course of a mountain pine beetle epidemic, that is, the amount and type of tree mortality, is shown in figure 6A and B. The two infestations, recorded under separate temporal and spatial conditions in northwestern Wyoming, have dramatic similarities. One can expect, with some variation, that a mountain pine beetle epidemic will follow this general pattern when site and stand conditions are similar.

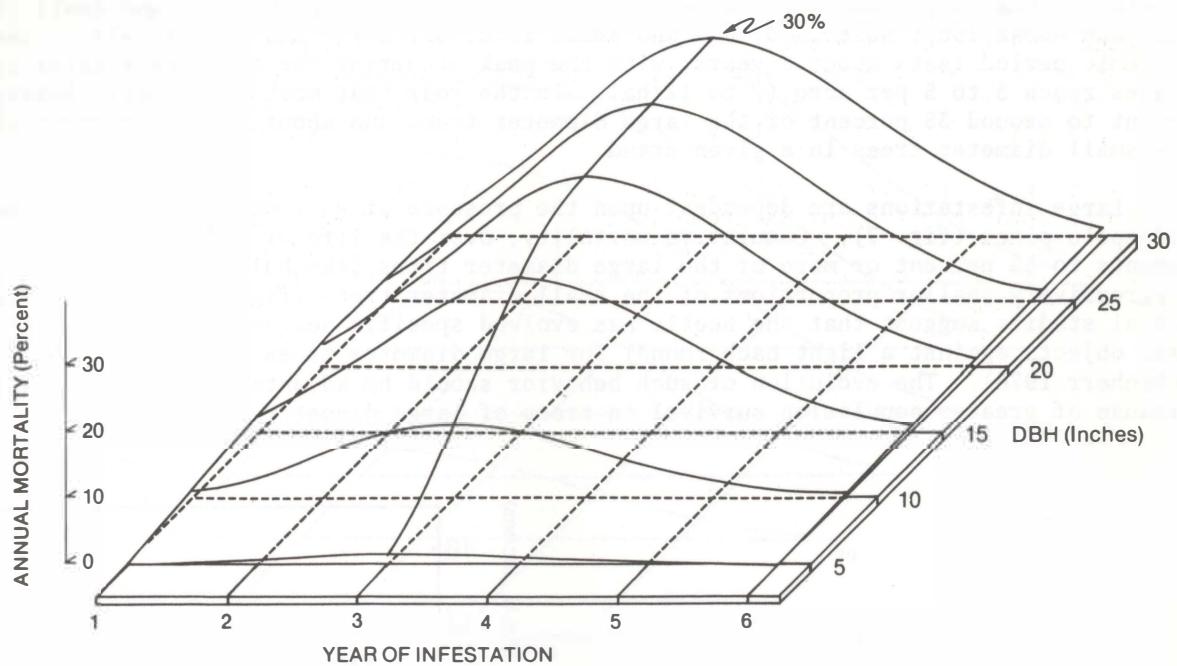


Figure 6A.--Annual mortality (percent) by diameter and year of infestation (Cole and others 1976).

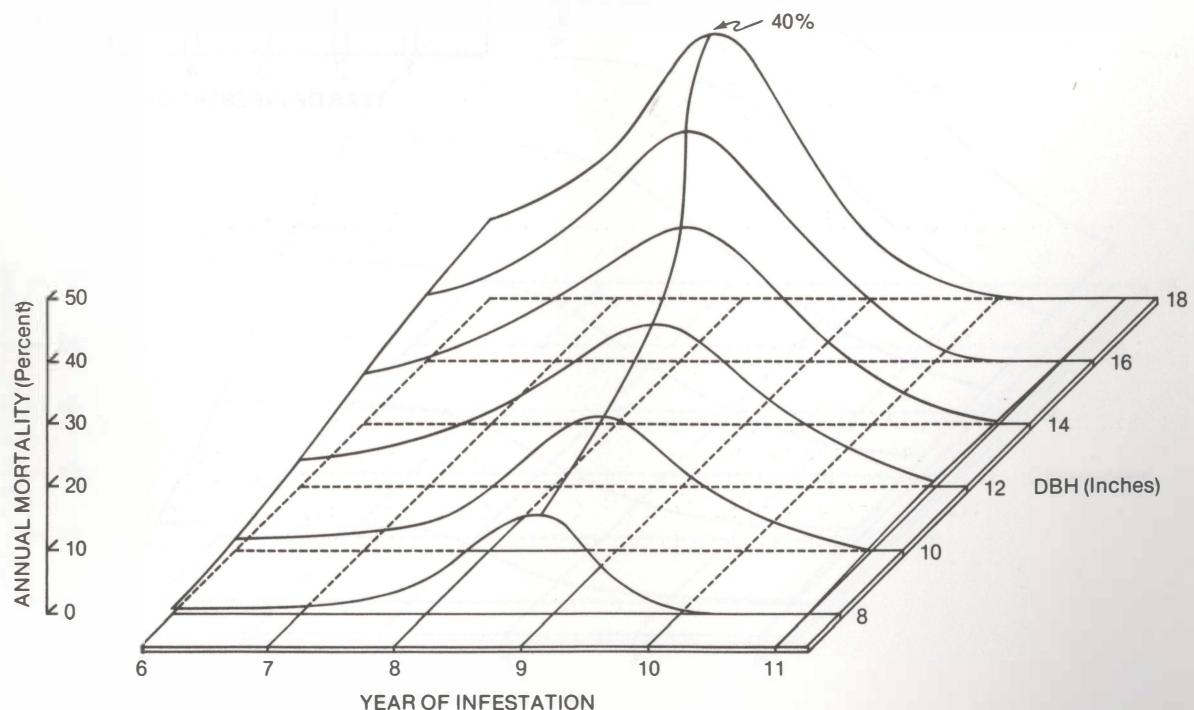
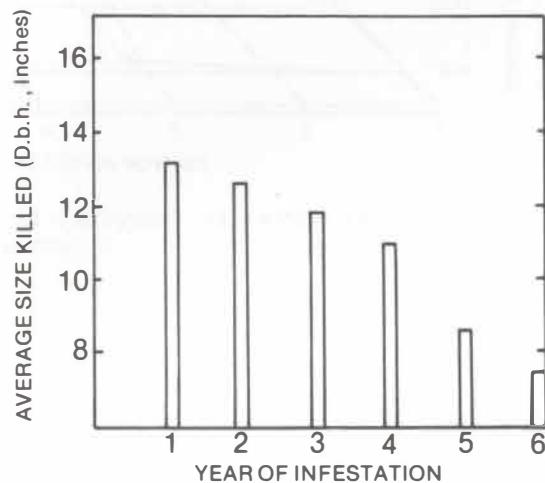


Figure 6B.--Annual mortality (percent) by diameter and year of infestation (Klein and others 1978).

Mortality of lodgepole pine over the main epidemic years is proportionately greater in the large diameter classes (Evenden and Gibson 1940; Hopping and Beall 1948; Cole and Amman 1969; Reid 1963; Roe and Amman 1970; Safranyik and others 1974). The epidemic period lasts about 6 years, with the peak occurring the third year after tree losses reach 3 to 5 per acre (7 to 12/ha). In the year that mortality peaks, losses amount to around 35 percent of the large diameter trees and about 5 to 10 percent of the small diameter trees in a given stand.

Large infestations are dependent upon the presence of at least some large diameter lodgepole pines (fig. 7). Cumulative mortality, over the life of an epidemic, frequently amounts to 85 percent or more of the large diameter trees (the bulk of the volume) and progressively smaller proportions of the small diameter trees (fig. 8A and B). Experimental studies suggest that the beetle has evolved specific searching behavior (large, dark objects against a light background) for large diameter trees (Shepherd 1966; Schonherr 1976). The evolution of such behavior should be advantageous to the beetle because of greater population survival in trees of large diameter.

Figure 7.--Average diameter of lodgepole pine trees killed by year of infestation in a northwestern Wyoming stand (Cole and Amman 1969).



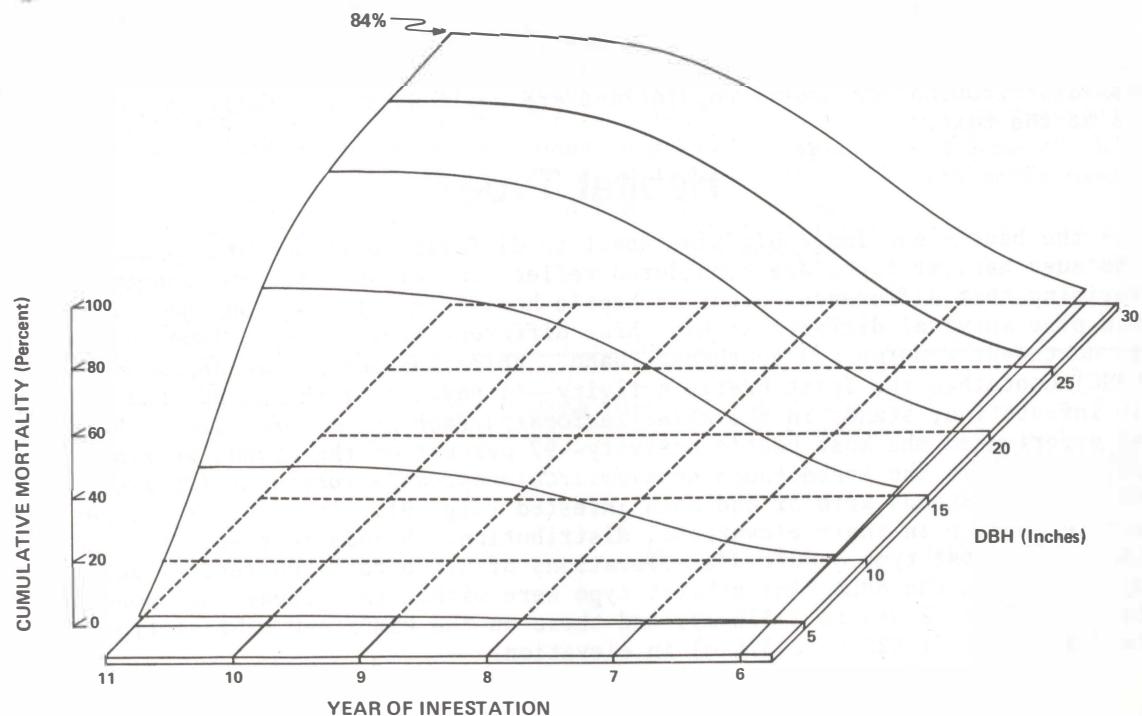


Figure 8A.--Cumulative mortality (percent) by diameter and year of infestation (Cole and others 1976).

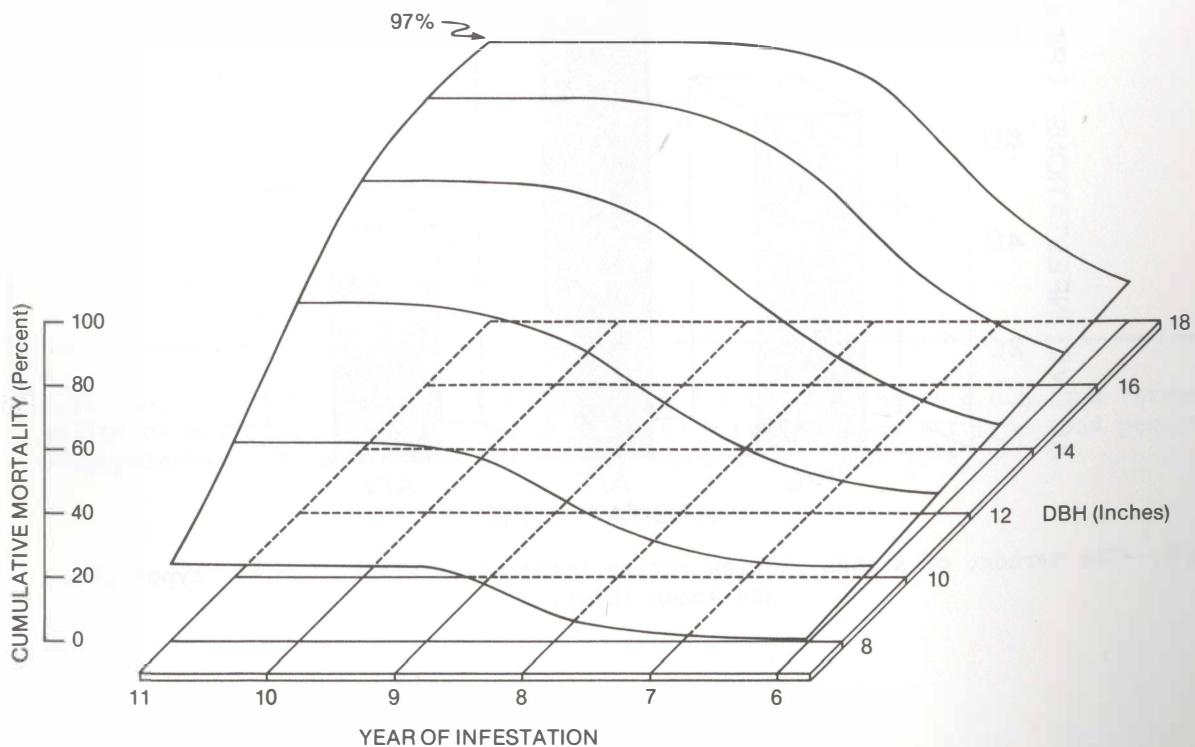


Figure 8B.--Cumulative mortality (percent) by diameter and year of infestation (Klein and others 1978).

Several factors influence this trend of loss within individual stands: diameter distribution within the stand (stand structure), phloem thickness distribution within diameter classes, habitat type, elevation, latitude, and beetle populations. Phloem thickness distribution and beetle populations are dealt with more fully in following portions of the text.

Habitat Type

Both the beetle and lodgepole pine react to different environments in characteristic ways. Because habitat types are considered reflections of specific environments, it is not surprising that differences occur in beetle-host interactions among habitat types. Lodgepole pine survival differed within three different habitat types (Roe and Amman 1970) in northwest Wyoming and southeast Idaho. *Abies lasiocarpa/Vaccinium scoparium* (ABLA/VASC) contained the least beetle activity--44 percent of the stands had experienced a beetle infestation; stands in the *Abies lasiocarpa/Pachistima myrsinites* (ABLA/PAMY) type had experienced the most beetle activity--92 percent of the stands were actively infested; and within the *Pseudotsuga menziesii/Calamagrostis rubescens* (PSME/CARU) type--64 percent of the stands were or had been infested (fig. 9). These habitat types showed considerable overlap in their elevational distribution. Stands that were examined on the ABLA/VASC habitat type occurred at elevations of 6,500 to 8,500 feet (1 982 to 2 591 m), stands on the ABLA/PAMY habitat type were within the elevational zone of 6,700 to 7,800 feet (2 043 to 2 378 m), and those on the PSME/CARU habitat type were 6,000 to 7,800 feet (1 829 to 2 378 m) in elevation.

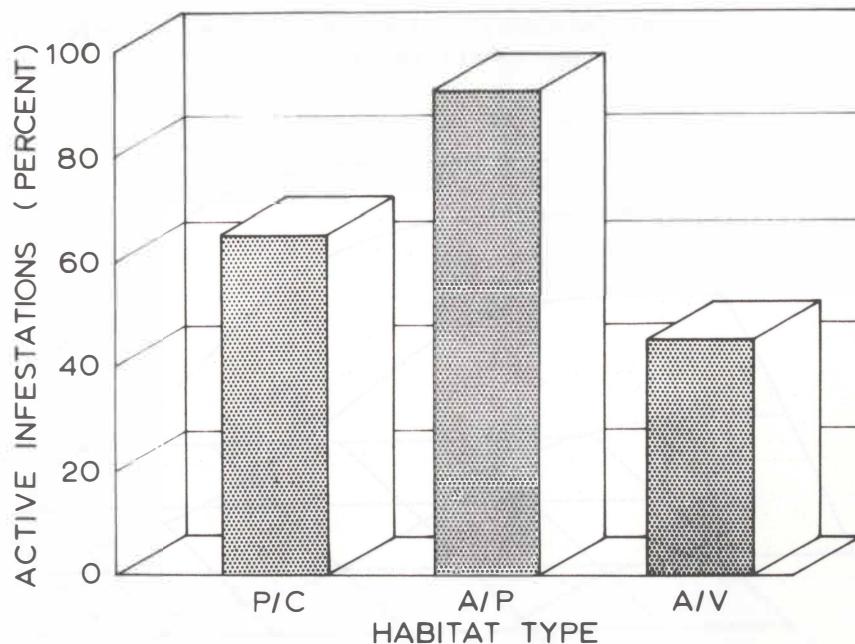


Figure 9.--The percent of stands showing active infestation within habitat types (Roe and Amman 1970).

"Mortality of lodgepole pine from mountain pine beetle also was found to be strongly related to habitat types (as defined by Pfister and others 1977) in the Gallatin Canyon of Montana (McGregor 1978). Habitat types were grouped into four classes and losses to mountain pine beetles were found to decrease in the following order--Douglas-fir, spruce, subalpine fir, and lodgepole pine climax (McGregor 1978). There was little difference, however, among Douglas-fir, spruce, and some of the sub-alpine fir types with losses ranging from 40 to 42 percent of the lodgepole pine basal area in trees 8 inches (20.3 cm) or more d.b.h. (fig. 10A and B).

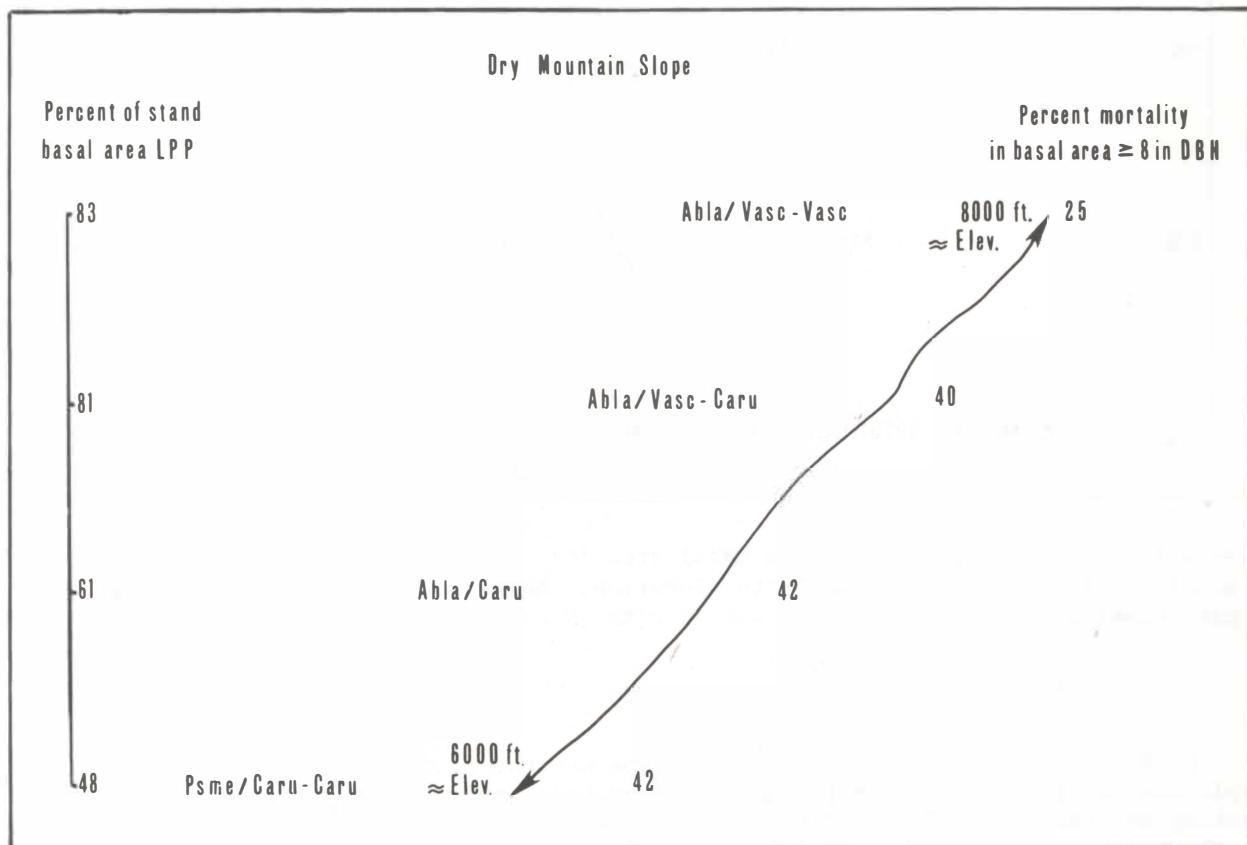


Figure 10A.--Percent lodgepole pine basal area for trees 8 inches d.b.h. and larger killed by mountain pine beetle in relation to elevation, habitat type, and percent lodgepole basal area in the stands on dry aspects (McGregor 1978).

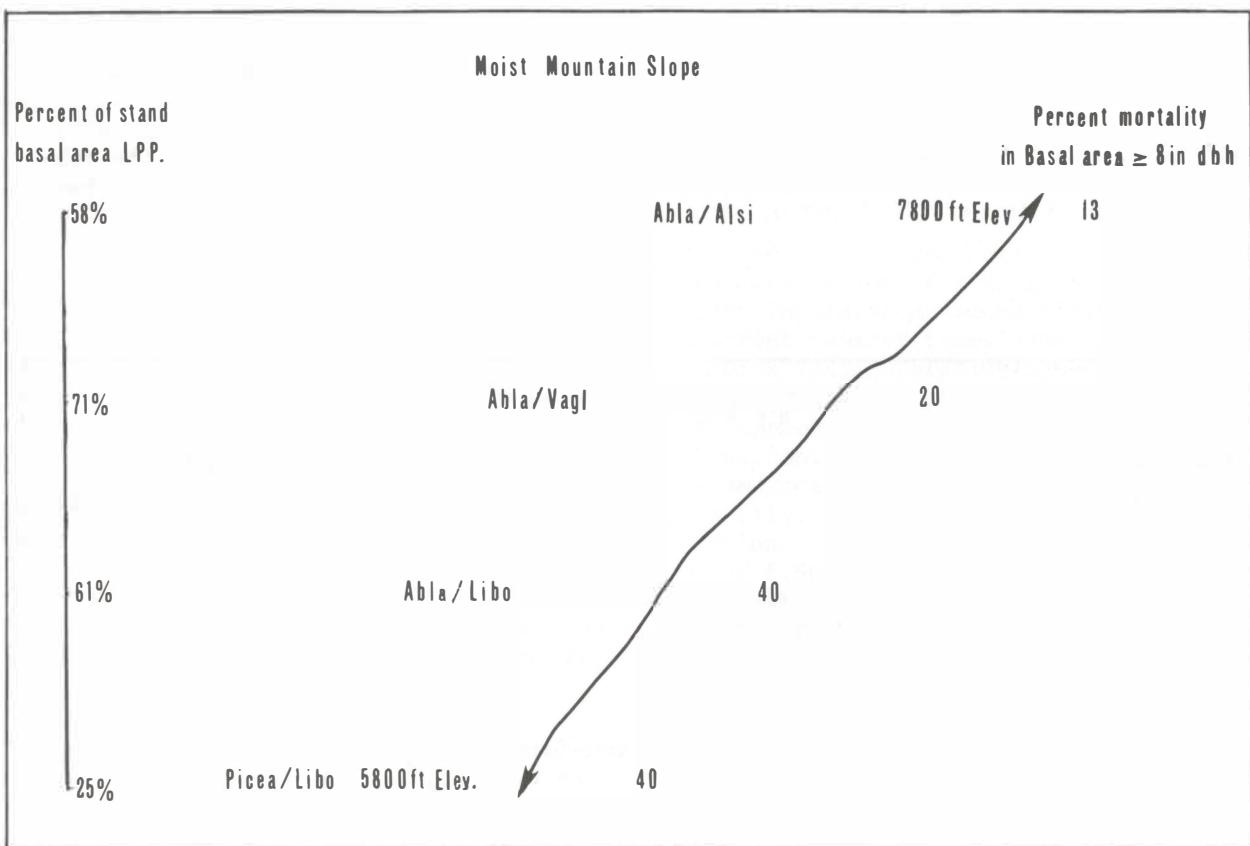


Figure 10B.--Percent lodgepole pine basal area for trees 8 inches and larger killed by mountain pine beetle in relation to elevation, habitat type, and percent lodgepole pine basal area in the stands on wet aspects (McGregor 1978).

D. M. Cole (1973) found that habitat type was the second most important variable explaining variance in phloem thickness (after basal area increment) in all higher ranking regressions of from two to six independent variables. Since phloem thickness is the most important factor in determining brood production of the mountain pine beetle, trees growing on the best sites can be expected to have thicker phloem on the average, which results in more frequent and more intense beetle infestations.

The effects of elevation are important when considering beetle behavior within and among habitat types.

Elevation

Brood production in bark of a given thickness is inversely related to elevation (fig. 11) (Amman 1969). Mountain pine beetle brood production and adult survival are low above 8,000 feet (2 439 m) at 43° N. latitude, where up to 2 years may be required for the beetle to complete its life cycle (Amman 1973). Consequently, mortality of lodgepole pine to the beetle is strongly related to elevation (Amman and Baker 1972; Amman 1975).

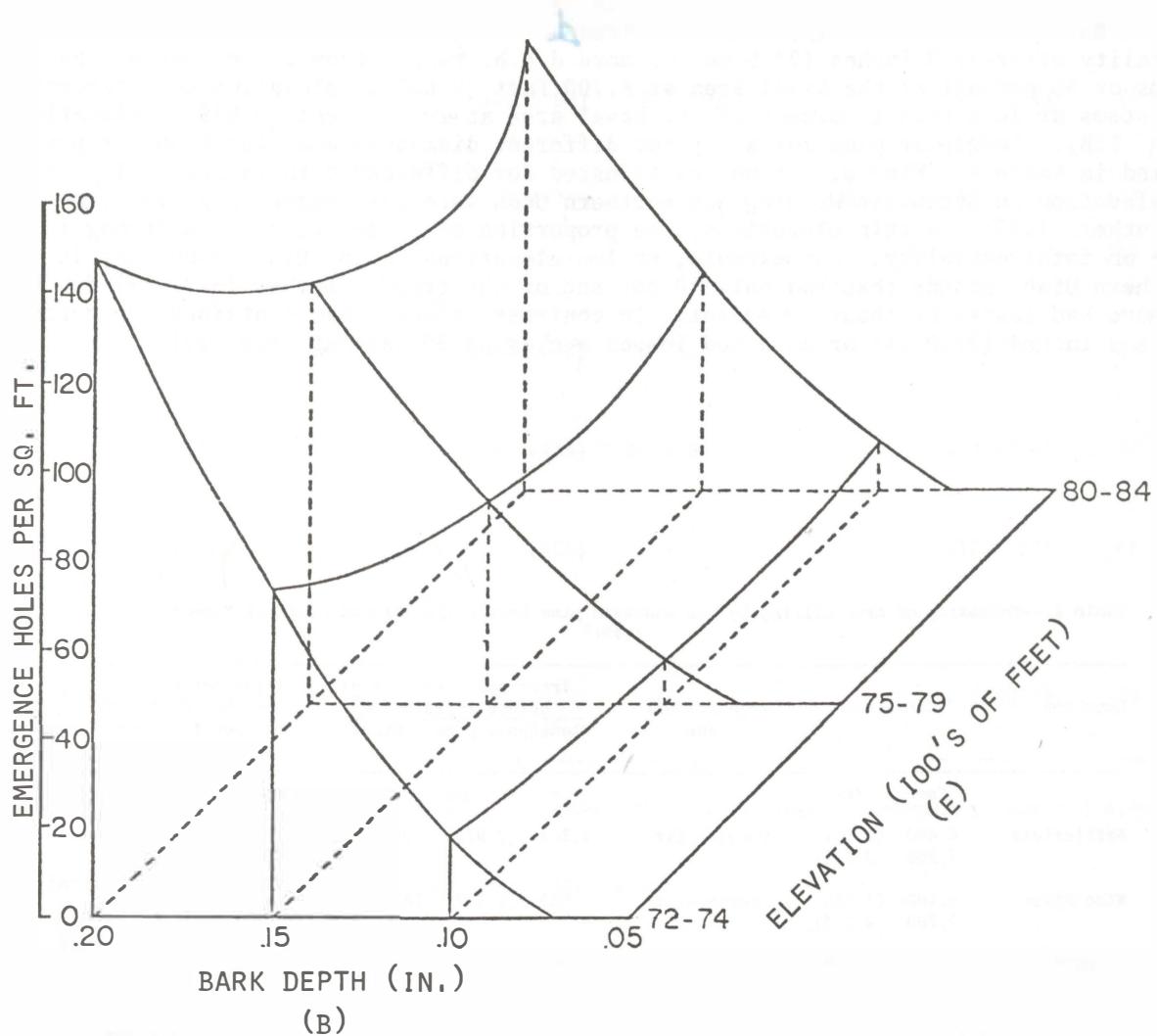


Figure 11.--The relation of mountain pine beetle emergence holes to bark thickness (measured in fissures) of lodgepole pine killed in 1964 at different elevations (Amman 1969).

Early work by Gibson² pointed to differences in beetle infestation intensity that are related to elevation. He reported that the infestations appeared to be less intensive on the upper end of his sample strips than on the lower. In the Beaverhead National Forest data (table 2), the Elkhorn strip sample, highest in elevation and in the subalpine fir-Engelmann spruce vegetational zone, showed the fewest beetle-killed trees. Data obtained by Gibson on the Bitterroot National Forest displayed the same trend, except in the plot at the lowest elevation (table 3). Mortality of trees 9 inches (22.9 cm) d.b.h. in northwest Wyoming and southeast Idaho averaged 80 percent at 6,400 feet (1 951 m) elevation, but only 20 percent at 9,200 feet (2 805 m) (Amman 1975) (fig. 12A). In northern Utah, a similar trend was noted (Amman and others 1973). Mortality of trees 9 inches (22.9 cm) or more d.b.h. ranged from 37 percent of the stems or 36 percent of the basal area at 8,700 feet (2 652 m) elevation to 2 percent of the stems or less than 1 percent of the basal area at 10,000 feet (3 049 m) elevation (fig. 12B). Lodgepole pine mortality for different diameters and elevations is presented in table 4. When elevation was adjusted for differences in latitude, losses by elevation in northwest Wyoming and northern Utah were comparable (fig. 13) (Amman and others 1973). Within elevations, the proportion of large trees has a strong influence on total mortality. For example, at low elevations in the Uinta Mountains in northern Utah, stands that had only 10 percent of the trees 9 inches (22.9 cm) d.b.h. or more had losses of about 2 percent. In contrast, stands that contained 100 percent trees 9 inches (22.9 cm) or more had losses averaging 30 percent (fig. 14).

Table 2--Intensity of tree killing by the mountain pine beetle (Beaverhead National Forest 1923-1940)¹

Location	Elevation	Vegetational zone	Trees per acre (per ha) before infestation ²		Trees per acre (per ha) killed by the mountain pine beetle	
			Lodgepole pine	Other	Number	Percent
Feet (m)			- - - - Number - - - -		Number	Percent
Battlefield	6,400- (1 941- 7,300 2 214)	Douglas-fir	1,203 (2 971)	21 (52)	209 (516)	17.4
Wise River	6,400- (1 941- 7,300 2 214)	Douglas-fir	533 (1 317)	180 (445)	46 (114)	8.6
Elkhorn	7,200- (2 184- 7,950 2 412)	Subalpine fir- Engelmann spruce	1,044 (2 579)	12 (30)	24 (59)	2.3

¹Compiled from data collected by Archie Gibson, USDA Forest Insect Laboratory, Coeur d'Alene, Idaho.

²Includes trees 3 inches (7.62 cm) d.b.h. and larger.

²Gibson, Archie L. 1943. Status and effect of a mountain pine beetle infestation on lodgepole pine stands. Unpubl. rep. 34 p. USDA For. Insect Lab., Coeur d'Alene, Idaho.

Table 3.--Intensity of tree killing by the mountain pine beetle (Bitterroot National Forest 1923-1940)¹

Plot	Elevation	Vegetational zone	Trees per acre (per ha) in spring 1923 ²			Trees per acre (per ha) killed by the mountain pine beetle		
			Lodgepole pine (LPP)	Douglas-fir	Ponderosa pine (PP)	Number	Number	Percent
Feet	(m)		----- Number -----					
A	5,400 (1 638)	Douglas-fir	320 (790)	32 (79)	--	272 (672)	272 (672)	85.0
B	5,400 (1 638)	Douglas-fir	32 (79)		136 (336)	LLP 32 (79)	100.0	
					PP 116 (287)		85.3	
C	5,100 (1 547)	Douglas-fir	260 (642)	72 (178)	--	216 (534)	216 (534)	83.1
D	6,000 (1 820)	Douglas-fir	172 (425)	40 (99)	--	140 (346)	140 (346)	81.9
E	7,100 (2 154)	Subalpine fir- Engelmann spruce	172 (425)	--	--	112 (277)	112 (277)	65.1
F	4,750 (1 441)	Douglas-fir	256 (632)	--	--	112 (277)	112 (277)	43.8

¹Compiled from data collected by Archie Gibson, USDA Forest Insect Laboratory, Coeur d'Alene, Idaho.

²Includes trees 3 inches (7.62 cm) d.b.h. and larger.

Figure 12A.--Tree survival from beetle infestation is directly related to elevation. These data obtained at 44° N. lat., 110° W. long. (Amman 1975).

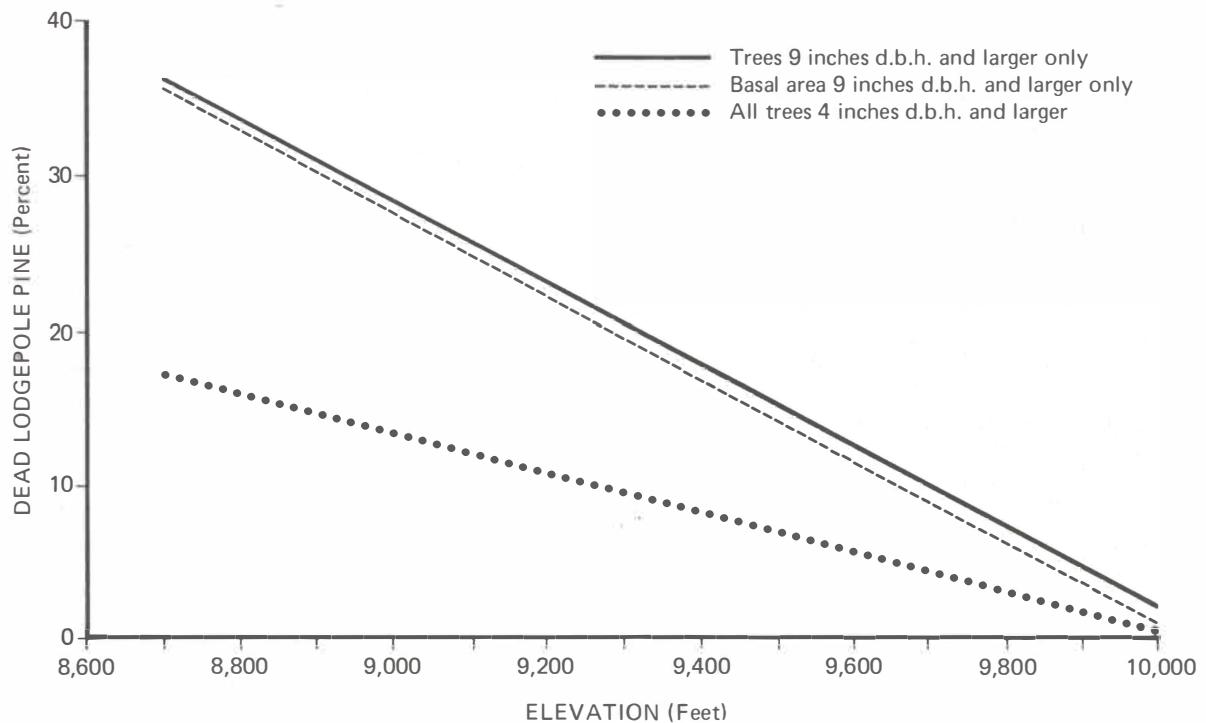
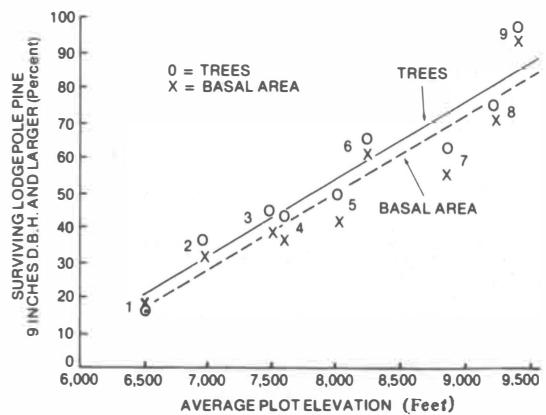


Figure 12B.--Proportions of lodgepole pine stems and basal area killed by the mountain pine beetle in relation to elevation on the north slope of the Uinta Mountains (Amman and others 1973).

Table 4.--Numbers¹ per acre of lodgepole pine trees surviving (S), killed by the mountain pine beetle (MPB), and by other causes (OC) in seven elevation levels on the north slope of the Uinta Mountains (Amman and others 1973).

Tree size (d.b.h.)	Elevation levels in feet (m)																				
	8,725-8,999 (2 647-2 729)			9,000-9,199 (2 730-2 789)			9,200-9,399 (2 790-2 850)			9,400-9,599 (2 851-2 911)			9,600-9,799 (2 912-2 972)			9,800-9,999 (2 973-3 033)			10,000-10,400 (3 034-3 155)		
	S	MPB	OC	S	MPB	OC	S	MPB	OC	S	MPB	OC	S	MPB	OC	S	MPB	OC	S	MPB	OC
<i>Inches (cm)</i>																					
4 (10.2)	40	0	1	47	³ <1	3	81	0	6	42	0	3	45	0	1	58	0	2	33	0	0
5 (12.7)	31	1	4	44	1	3	68	0	7	47	<1	3	42	0	2	45	0	4	34	0	4
6 (15.2)	19	3	0	36	1	1	56	1	5	35	1	3	46	1	2	42	0	1	40	0	1
7 (17.8)	18	6	1	28	1	2	34	2	3	33	2	3	41	0	2	36	0	<1	39	0	1
8 (20.3)	16	6	<1	17	1	2	29	2	<1	33	4	3	36	2	1	31	<1	<1	36	0	1
9 (22.9)	12	7	1	13	3	<1	22	3	1	21	2	1	28	1	1	21	<1	0	24	0	3
10 (25.4)	6	4	<1	11	4	1	13	2	1	14	2	1	16	3	1	22	<1	<1	24	1	1
11 (27.9)	3	3	0	11	2	0	9	2	0	10	2	2	13	3	1	14	<1	0	21	0	1
12 (30.5)	7	1	0	7	2	0	6	3	0	8	3	0	8	2	1	9	0	0	18	0	0
13 (33.0)	2	2	0	2	2	0	2	1	1	4	1	0	4	1	1	5	0	0	11	0	0
14 (35.6)	<1	0	0	2	1	0	1	1	0	3	0	0	3	1	0	4	0	0	11	0	0
15 (38.1)	1	0	0	2	<1	0	2	1	0	2	<1	0	1	<1	0	5	0	0	9	0	1
16+ (40.6+)	1	<1	0	1	1	0	1	2	0	5	2	0	3	2	<1	3	0	<1	8	0	0
Total trees per acre (per ha) ⁴	197 (487)			248 (613)			366 (904)			293 (724)			311 (768)			308 (761)			320 (790)		

¹Numbers rounded to the nearest whole number except when less than one-half tree per acre.

²Number of 1/10-acre plots.

³<1 indicates less than one-half tree per acre.

⁴Number recorded on 1/10-acre plots, not summation of rounded numbers in this table.

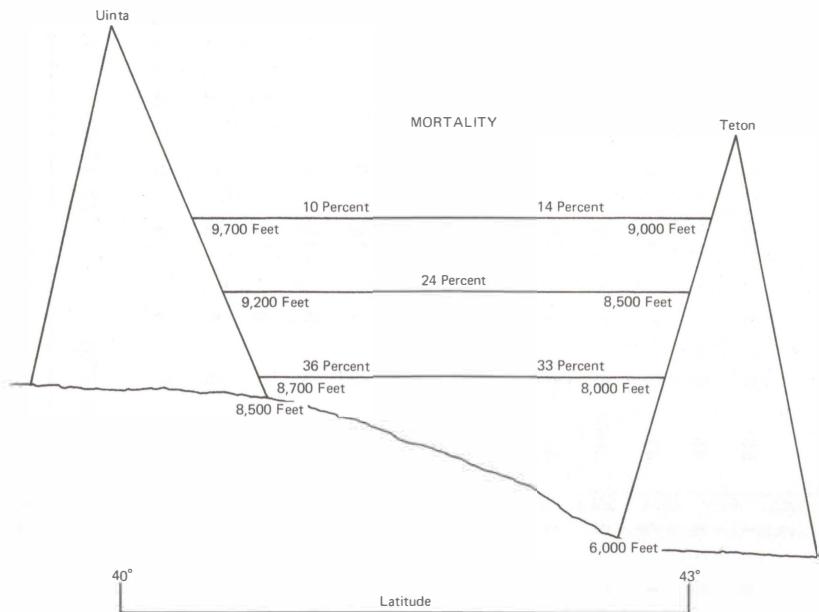


Figure 13.--Mortality of lodgepole pine in the Teton-Targhee area and north slope of the Uinta Mountains attributable to the mountain pine beetle was approximately equal when elevation is corrected for differences in latitude (Amman and others 1973).

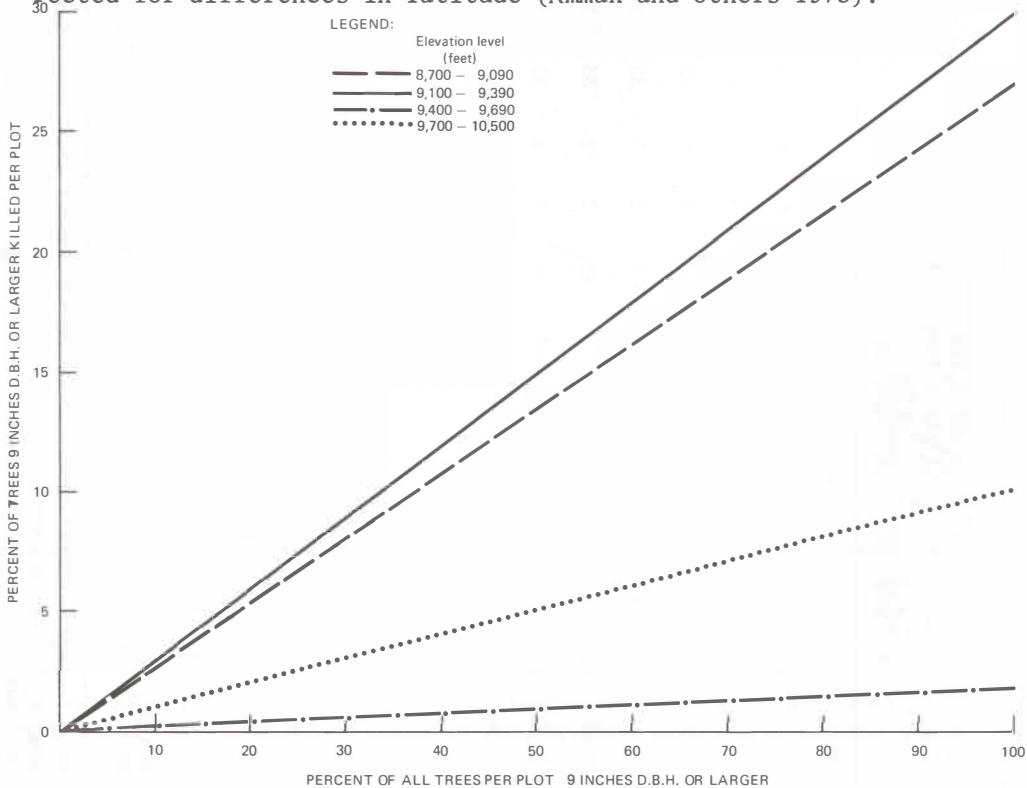


Figure 14.--Proportion of lodgepole pine trees 9 inches (22.9 cm) d.b.h. and larger killed by the mountain pine beetle in each 1/10-acre plot at different elevations in relation to the proportion of all lodgepole pine trees (4 inches [10.1 cm] d.b.h. or larger) that were 9 inches (22.9 cm) and larger in each 1/10-acre plot on the north slope of the Uinta Mountains (Amman and others 1973).

Losses within a given habitat type also were found to vary according to elevation (McGregor 1978). For example, losses of trees 8 inches (20.3 cm) or more d.b.h. within the xeric fir types varied from 42 percent at 6,000 feet (1 829 m) elevation to 25 percent at 8,000 feet (2 439 m) elevation in the Gallatin Canyon (fig. 10A).

Risk of tree losses to the beetle in western Canada also has been related to climatic zones (Safranyik and others 1974; Safranyik 1978) with the greatest mortality occurring at low elevations in southern British Columbia. Various weather observations were used to develop a hazard map and predict the probability of a beetle outbreak (Safranyik and others 1975). An attempt to extend the British Columbia hazard map into the United States was unsuccessful³. Climatic conditions in the low elevation lodgepole pine stands of the United States are rarely severe enough to restrict establishment and survival of the beetles.

The principal cause for variation in mortality of lodgepole pine among elevations is related to differences in climatic conditions that occur within the elevational strata; specifically, the effects of such differences on beetle biology and survival (Amman 1973; Safranyik 1978). At high elevations on the Bridger-Teton National Forest, for instance, cool temperatures delayed development so that a large proportion of the beetle population entered the winter as eggs, and first and second instars. In these stages, under subfreezing conditions, mortality is greater than in third and fourth instars (Amman 1973).

In stands on the Wasatch National Forest, Utah, the number and proportion of large lodgepole pine trees per acre (0.4 ha) and phloem thickness increased with elevation (Amman and others 1973) (table 5). Based on stand conditions alone, stands at the higher elevations should have been more susceptible to buildup of beetle populations than stands at the lower elevations; large infested trees usually produce more beetles per unit area of bark than do small trees (Reid 1963; Cole and Amman 1969). Climate at the higher elevations had an adverse effect on the beetle, however, keeping populations and hence tree losses at low levels. Nonetheless, where climatic factors do not limit beetle populations, the factors of tree size and phloem thickness assume paramount importance.

Table 5.--Number¹ and proportion of samples 0.11 inch (0.3 cm) or more thick per acre by diameter class, and average phloem thickness in inches (cm) of all phloem samples for lodgepole pine 9 inches (23 cm) d.b.h. and larger (Amman and others 1973)

Elevational level	Diameter class in inches (cm)								Total samples 0.11+	Phloem thickness all samples	
	9-10 (23-25)		11-12 (28-30)		13-14 (33-36)		15-16+ (38-41+)				
Feet (m)	No.	Percent	No.	Percent	No.	Percent	No.	Percent	Mean	Standard deviation	
8,800 (2 669)	12	33	13	64	3	60	2	38	30	0.105 (0.267)	0.0030
9,000 (2 730)	18	37	15	42	5	57	5	83	43	.104 (. 264)	.0036
9,200 (2 791)	23	33	17	57	4	72	4	64	48	.104 (. 264)	.0033
9,400 (2 851)	17	25	20	55	6	53	9	61	52	.103 (. 262)	.0036
9,600 (2 912)	44	50	20	48	7	46	2	20	73	.106 (. 269)	.0034
9,800 (2 973)	35	41	23	47	10	54	10	61	78	.110 (. 279)	.0039
10,000 (3 033)	37	39	39	50	17	38	20	59	113	.105 (. 267)	.0041

¹Two samples were taken per tree.

³Crookston, N. L. 1977. Mountain pine beetle (*Dendroctonus ponderosae* Hopkins, Coleoptera: Scolytidae) outbreaks in lodgepole pine (*Pinus contorta* Dougl.) and application of a climatic hazard rating to the Pacific Northwest. M.S. thesis, Univ. Idaho, Moscow. 91 p.

Tree Size

Beetle infestations measured in Forest Service Regions 4 and 2 rose from approximately 0.5 to 5.0 trees per acre (1.2 to 12.4/ha), in the early years, to a peak of 26 to 31 trees per acre (64.2 to 76.6/ha); then declined to 2 to 3.5 trees per acre (4.9 to 8.6/ha) after most of the larger diameter trees had been killed. Infestations in Region 1 (the Northern Region) were more intense. An epidemic lasts approximately 6 years. Once infestations build up, however, a large amount of beetle immigration may occur, resulting in more rapid tree losses and a shorter epidemic period in adjacent stands (table 6) (McGregor 1978).

Table 6.--Percent of lodgepole pine basal area killed by mountain pine beetle in stands infested for different numbers of years (McGregor 1978)

Years infested	Total basal area all species		Basal area killed, lodgepole pine		Percent
	Ft ²	(m ²)	Ft ²	(m ²)	
1	2,968	(267)	240	(22)	8
2	1,013	(91)	274	(25)	27
3	1,493	(134)	300	(27)	20
4	1,420	(128)	268	(24)	19
5	2,137	(192)	454	(41)	21
6	1,586	(143)	457	(41)	29
8	625	(56)	156	(14)	25

Large trees not only produce more beetles per unit area of bark but also more per tree because of their greater circumference and greater height of infestation (fig. 15) (Cole and Amman 1969; Reid 1963), which is related to tree diameter (fig. 16) (Cahill 1960). Height of attack also varies according to site quality because trees are taller on good sites (fig. 17)⁴. Numbers of beetles produced in trees of different sizes show that beetle production could vary from 300 for trees 8 to 9 inches (20.3 to 22.9 cm) d.b.h. to more than 18,000 for trees 18 inches (45.7 cm) d.b.h. (Cole and Amman 1969; Klein and others 1978).

⁴Johnson, Philip C. 1951. Height of broods as a factor affecting the treatment of standing lodgepole pine trees infested by the mountain pine beetle. Unpubl. rep., 8 p. USDA, Agric. Res. Serv., Bur. of Entomol. and Plant Quar., For. Insect Lab., Coeur d'Alene, Idaho.

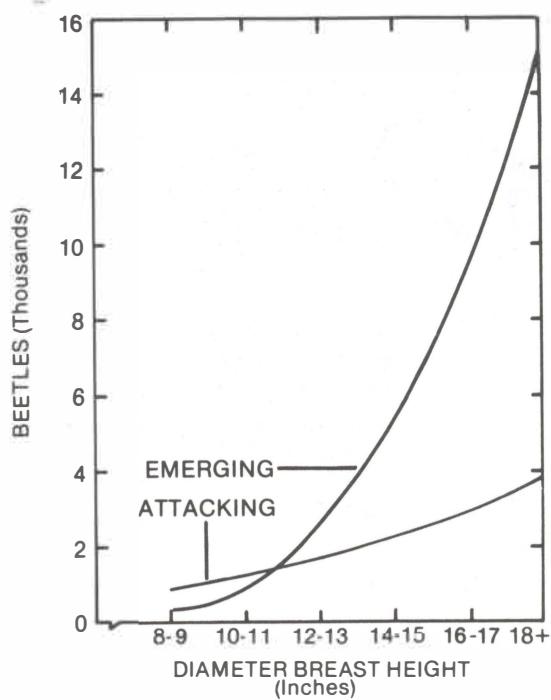


Figure 15.--Generally, the larger the tree, the larger the ratio of brood adults (emerging) to parents attacking and killing the tree (Cole and Amman 1969).

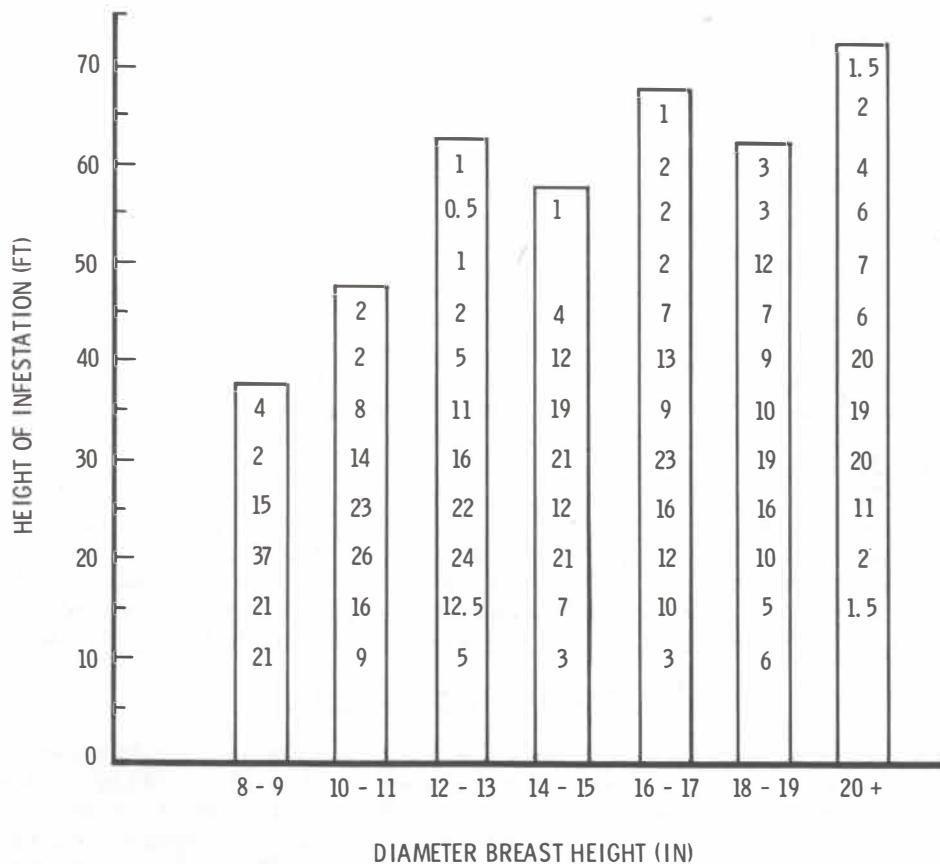


Figure 16.--Maximum height of attack expressed as percentage of trees within diameter classes, north slope of Uinta Mountains, Utah (Cahill 1960).

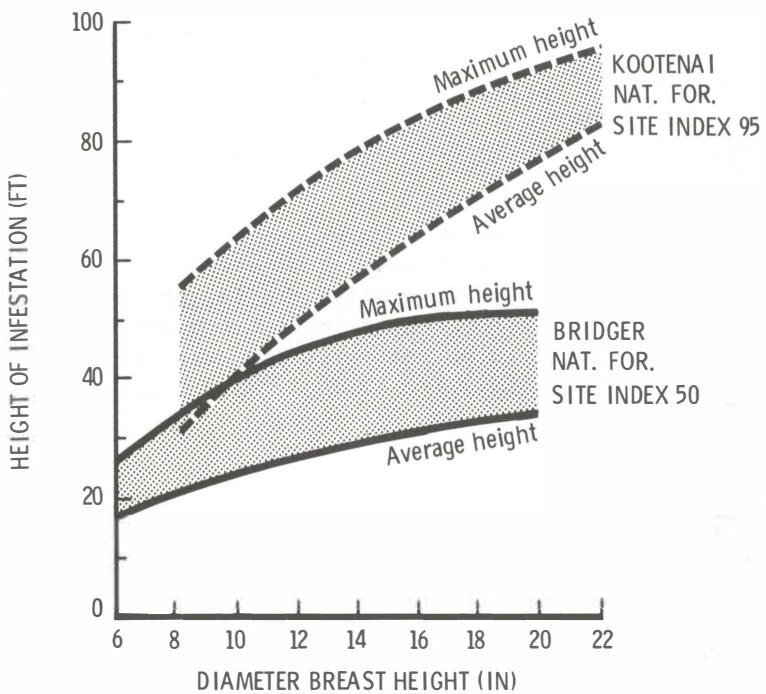


Figure 17.--The maximum height and average height of mountain pine beetle infestation in lodgepole pine growing on different forest sites. (From Johnson, see footnote⁴.)

Assuming an infestation rate of 12 female beetles/ ft^2 (929 cm^2) of bark surface, a rate commonly observed in the field, and a 1:1 sex ratio, 24 beetles/ ft^2 (929 cm^2) would be sufficient to infest and kill a tree. Thus, a tree 8 to 9 inches (20.3 to 22.9 cm) d.b.h. would produce only one-third enough beetles to infest and kill a tree with a 12-inch (30.5-cm) d.b.h. In a northwest Wyoming stand, only trees 12 to 13 inches (30.5 to 33.0 cm) d.b.h. produced on the average more emerging than attacking beetles. If we assume that one-third to one-half of the beetles that emerged failed to make successful attacks, then only trees 14 inches (35.6 cm) or larger d.b.h. produced on the average enough beetles to increase the infestation or maintain it at the previous year's level. This relationship could be expected to vary somewhat from stand to stand depending upon site quality, stocking level, and elevation-latitude.

Phloem Thickness

The thickness of phloem within trees of a stand determines whether the insect can maintain or increase its numbers. Phloem thickness is strongly related to diameter of lodgepole pine trees (fig. 18), but this relation varies from stand to stand because of stand and site factors (table 7). Phloem thickness is functionally related to tree vigor as expressed in basal area increment (D. M. Cole 1973). Phloem thickness also was positively correlated with habitat type, elevation, total tree height, and age (D. M. Cole 1973).

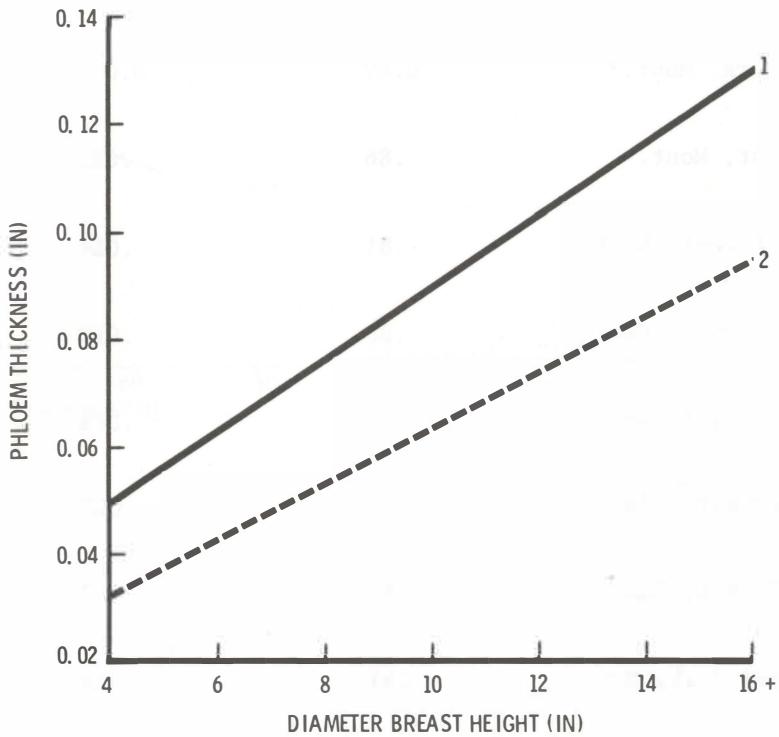


Figure 18.--Phloem is usually thicker in large than small diameter trees and differs by stand as illustrated by these two stands in western Montana: (1) Lazier Creek, Lolo National Forest, $\hat{Y} = 0.0232 + 0.0067X$, $r^2 = 0.86$; (2) Solo Joe Creek, Kootenai National Forest, $\hat{Y} = 0.0118 + 0.0052X$, $r^2 = 0.88$. These data kindly furnished by Mark D. McGregor, Entomologist, Forest Service, Forest Insect and Disease Management, Missoula, Mont.

Table 7.--Relation of phloem thickness to d.b.h. of lodgepole pine trees (Amman 1978)

Plot location	Coefficient of determination (r^2)	Y intercept	Regression coefficient
Camas Creek Glacier National Park, Mont. ¹	0.69	0.036	0.0031
Lazier Creek Lolo National Forest, Mont.	.86	.023	.0067
Calyx Creek Kootenai National Forest, Mont.	.81	.034	.0038
Solo Joe Kootenai National Forest, Mont.	.88	.012	.0052
West Yellowstone Gallatin National Forest, Mont.	.95	.043	.0050
Pineview Targhee National Forest, Idaho	.77	.057	.0033
Warm River Targhee National Forest, Idaho	.88	.027	.0066
Signal Mountain Grand Teton National Park, Wyo.	.91	.038	.0059
Black Rock Creek Teton National Forest, Wyo.	.77	.028	.0058
Bear River Wasatch National Forest, Utah	.70	.060	.0042

¹Mark D. McGregor, Entomologist, Forest Service, Forest Insect and Disease Management, Missoula, Mont., kindly furnished data from Camas, Lazier, Calyx, and Solo Joe areas.

Stand density affects the growth rate of trees, and hence phloem thickness. Generally, stands having the lowest density have trees with the thickest phloem (fig. 19). Because average phloem thickness is greater, beetle production will also be greater in trees of each diameter class in more open stands (fig. 20). Consequently, tree mortality in these stands will be proportionately greater than those in dense stands.

Beetles have been observed to select trees that possessed the thickest phloem in a stand where trees had similar d.b.h. In addition, beetles often selected that portion of an individual tree that had the thickest phloem (Roe and Amman 1970). These points are dealt with more fully in following portions of the text.

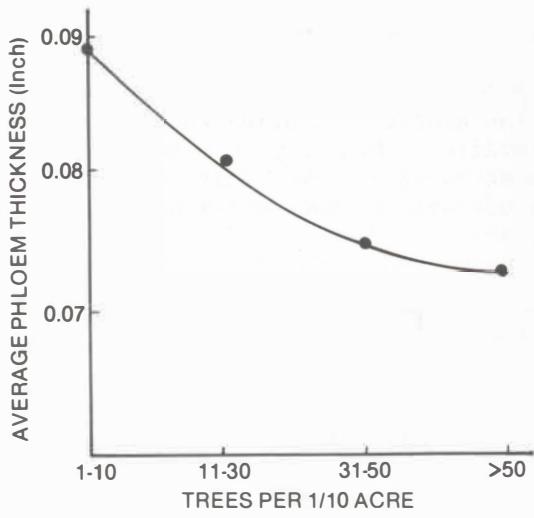


Figure 19.--Trees in dense stands have thinner phloem than those in open stands (Amman and others 1977).

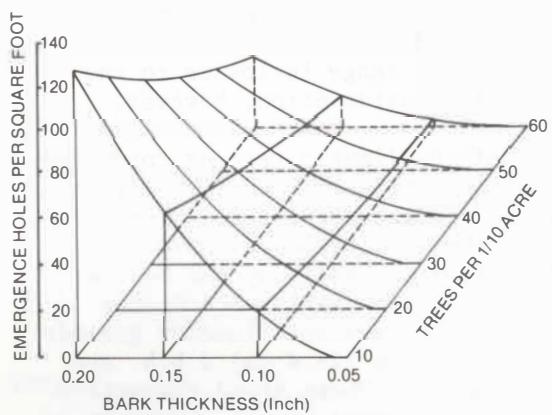


Figure 20.--Beetle production is less in trees of dense stands. Such trees have thinner bark and lower average phloem thickness. Generally, as total bark thickness increases, phloem thickness also increases (Amman 1969).

UNIFIED CONCEPT OF BEETLE-TREE INTERACTION

The mountain pine beetle is food limited in those stands of lodgepole pine where developmental temperatures are optimum (Cole and Amman 1969); only trees that have a certain thickness of phloem usually produce enough beetles to keep an infestation going. When beetles have killed most of the trees that have thick phloem, they attack smaller trees that generally have thin phloem. Thin phloem coupled with excessive drying of the tree results in high brood mortality. The beetle population thus declines. Where climatic factors are severe, such as at high elevations, beetle populations are adversely affected, regardless of tree size. This constitutes a basic limit of population growth and establishes geographical as well as elevational boundaries beyond which epidemic beetle populations can seldom develop.

DETERMINING STAND SUSCEPTIBILITY

A number of risk rating systems have been devised during recent years and some have been partially tested. Most of the systems are attempts to classify observed or historical losses to the beetle under a variety of tree, stand, and site conditions.

One of the simplest systems is to map past beetle infestations for a region (Crookston and others 1977). Such a map directs land managers to areas where repeated mountain pine beetle infestations have occurred. In such areas, stands then can be risk rated using some of the stand specific hazard rating systems developed by others.

Expected tree losses to the beetles have been related to habitat types (Roe and Amman 1970). The risk of growing trees to a specific diameter was considered the product of the proportion of trees killed in a diameter class times the proportion of stands on a given habitat type that showed prior evidence of having been infested. For example, growing trees to 16 inches (41 cm) d.b.h. would be a high risk on ABLA/PAMY type where 82 percent of the trees were killed and 92 percent of the stands were infested ($82 \times 92 = 75$ percent probability of loss) with only 25 percent or less expected survival of 16-inch (40.6-cm) d.b.h. trees. In contrast, the risk of growing 16-inch (40.6-cm) d.b.h. trees on the ABLA/VASC type is much less ($82 \times 44 = 36$ percent probability of loss) with about two-thirds of the trees expected to survive. Because of the elevational range in some habitat types and corresponding range in losses to the beetles (McGregor 1978), elevation must also be taken into consideration, however.

Safranyik and others (1974) used weather data to define climatic regions conducive to mountain pine beetle infestations in British Columbia. Within regions susceptible to outbreaks, stands then were evaluated on the basis of age and size. The observations of Shrimpton (1973) show a reduction at about age 80 in the resistance response of trees to inoculations of a blue-stain fungus that is carried naturally by the beetle. These inoculations were used as an indirect measure of the trees' resistance to the beetle. Safranyik and others (1974) state that stands with an average diameter greater than 8 inches (20.5 cm), or containing many trees over 10 inches (25.4 cm) d.b.h. and older than 80 years, have the potential for a beetle epidemic. These stand characteristics seldom occur until the current annual increment and the mean annual increment of the stand are equal, thus suggesting a physical yield rotation is attainable before the stand is highly susceptible.

Usually factors governing beetle brood production are ignored or are inadvertently accounted for in stand measurements without an understanding of the biological implication in development of stand risk rating systems. Beetle brood production is correlated positively with phloem thickness (food supply for developing larvae) (Amman 1969; 1972) and phloem thickness is correlated positively with tree diameter (Amman 1969; 1975; D. M. Cole 1973). These characteristics of diameter and phloem thickness were used to assess beetle population potential within three Colorado stands, and in themselves constitute a risk rating system (W. E. Cole 1978; Cole and Cahill 1976).

In a stand located at Hot Sulphur Springs, which had just been subjected to a mountain pine beetle epidemic and was reconstructed on paper as a "green stand," a direct accounting of the beetle population focuses specifically on trees 10 inches (25.4 cm) or more d.b.h. An estimated 89 percent of emerging brood adults came from these trees and an estimated 69 percent of all brood adults came from trees 12 inches (30.5 cm) or more d.b.h. (table 8). These figures show the importance of the large diameter component of the stand to beetle brood production. In this same stand, the infestation resulted in the death of all trees 12 inches (30.5 cm) or more d.b.h. (table 9) and only 3 percent of the trees 10 inches (25.4 cm) or more survived beetle activity; however, half of these survivors had phloem thickness 0.11 inch (2.79 mm) or more. This phloem thickness on the average will produce enough brood to keep the infestation going at about the same level. Thicker phloem will result in a surplus of beetles (surplus is the number over and above the number of parents needed to kill the trees). The probability of intense beetle activity continuing in this stand was small because suitable host trees (large diameter trees with thick phloem) were almost exhausted (fig. 21).

Table 8.--Percentage distribution of attacking and emerging populations of mountain pine beetle among lodgepole pine by tree diameter and phloem thickness; data based on the number of parent attacks and of brood emergence holes (Cole and Cahill 1976)

Phloem thickness <i>inches (cm)</i>	Diameter at breast height in inches (cm)					Total	
	<7 (18)	8-9 (20-23)	10-11 (25-28)	>12 (>30)			
Attacking population							
Inches (cm)							
<0.11 (<0.28)	7	15	18	20	60		
≥ .11 (≥ .28)	1	3	7	29	40		
Total	8	18	25	49	100		
Emerging population							
<0.11 (<0.28)	1	5	10	15	31		
≥ .11 (≥ .28)	1	4	10	54	69		
Total	2	9	20	69	100		

Table 9.--Percent infestation and phloem class by diameter class, for three infestation areas (Cole and Cahill 1976)

Stand	Percent postinfestation stand by diameter class in inches (cm)			Percent trees containing ≥ 0.11 inch (.28 cm) phloem by diameter class in inches (cm)		
	≥ 8 (20)	≥ 10 (25)	≥ 12 (30)	≥ 8 (20)	≥ 10 (25)	≥ 12 (30)
Hot Sulphur Springs	18	3	0	29	50	0
Strawberry Creek	41	20	8	19	23	27
Buffalo Peak	66	40	17	45	51	72

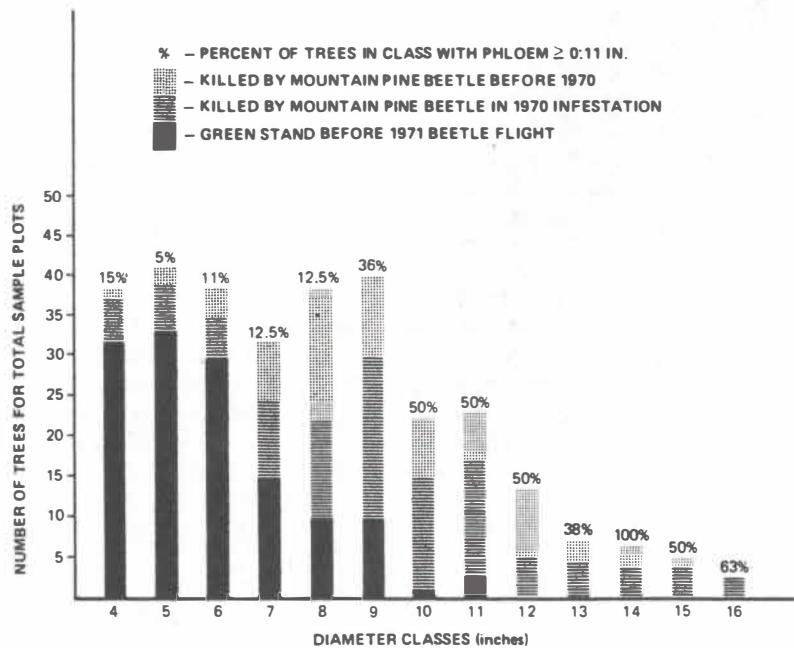


Figure 21.--Lodgepole pine diameter and phloem thickness distributions within the Hot Sulphur Springs, Colo., stand after 5 years of mountain pine beetle infestation.

A second stand (Strawberry Creek) experienced only light beetle infestation. Eight percent of the trees were 12 inches (30.5 cm) or more d.b.h. (table 9) and there was only a 27 percent chance that any tree over 12 inches (30.5 cm) d.b.h. would contain phloem 0.11 inch (2.79 mm) or more thick (fig. 22). Tree mortality in this stand has continued to be small (Donn B. Cahill, personal communication, April 1978).

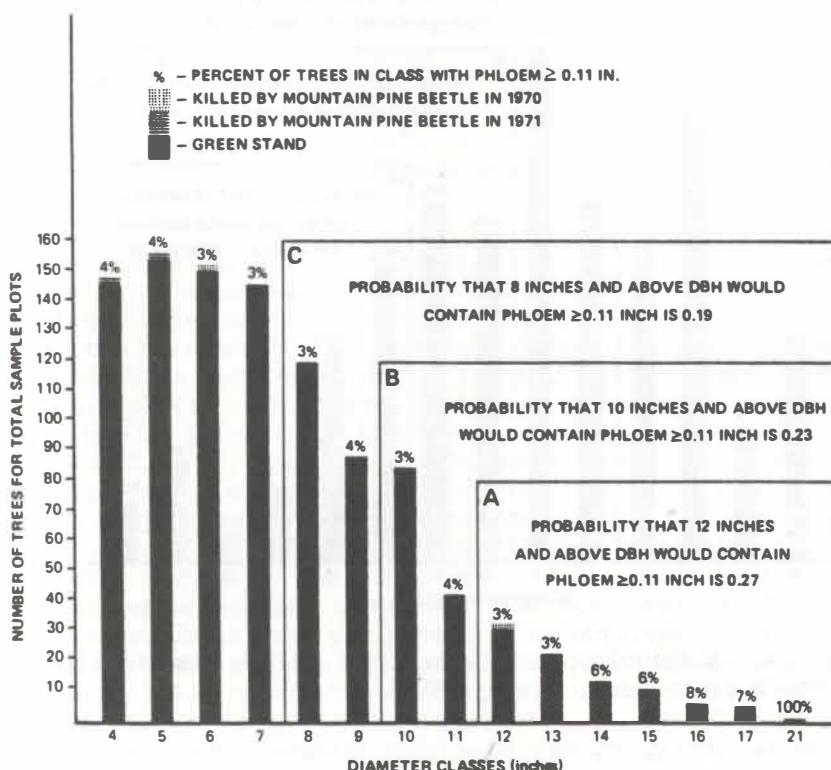


Figure 22.--Lodgepole pine diameter and phloem thickness distributions within the Strawberry, Colo., stand after 5 years of mountain pine beetle infestation.

In a third stand (Buffalo Peak), great potential existed for a beetle infestation. Within this stand, 17 percent of the trees were 12 inches (30.5 cm) or more d.b.h. (table 9) with a 72 percent chance that any one tree in this class would contain phloem 0.11 inch (2.79 mm) or more thick. This high potential not only existed in the large diameter trees, but also in the 10- and 11-inch diameter classes (25.4-27.9 cm) as well where a 51 percent chance existed for phloem to equal or exceed 0.11 inch in thickness (fig. 23). Observations in these Colorado stands suggest that when about 25 percent of the trees 8 inches (20.8 cm) or more d.b.h. in a stand have phloem 0.11 inch (2.79 mm) or more thick, the stand has potential for a significant beetle outbreak and should be considered for harvesting.

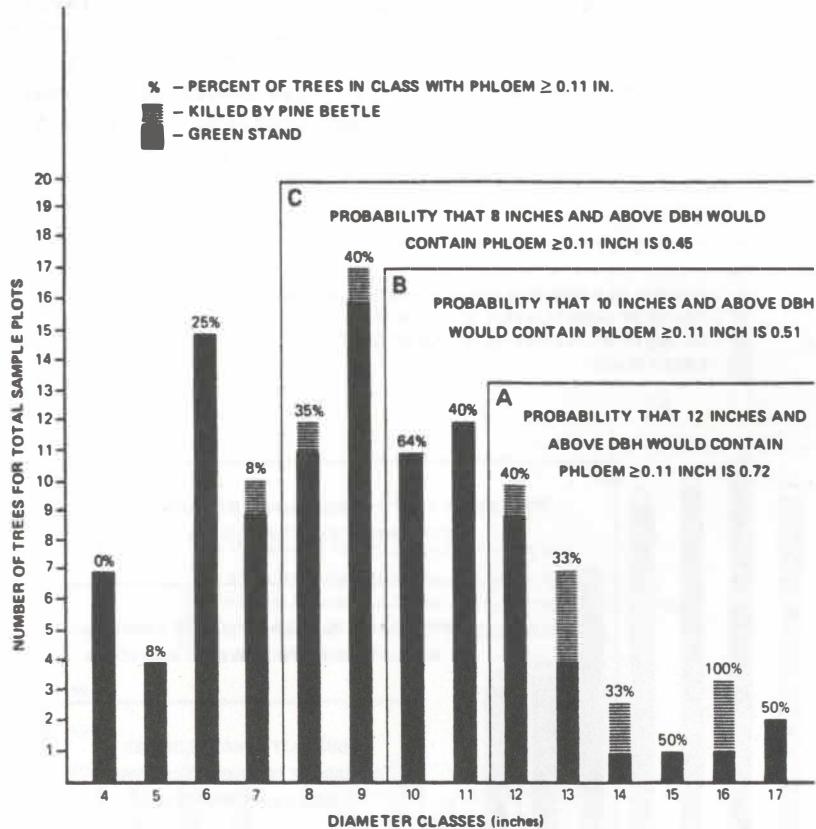


Figure 23.--Lodgepole pine diameter and phloem distributions in the Buffalo Peak, Colo., stand.

Stand characteristics consisting of crown competition factor (CCF) and percent of the basal area that is lodgepole pine were used for a stand hazard rating (SHR) system for stands in western Montana and northwestern Idaho (Schenk and others unpublished, but cited by Mahoney [1978]). The formula for SHR is:

$$\text{SHR} = \text{CCF} \times \frac{\% \text{ LPPBA}}{100}$$

Mahoney (1978) reported good agreement between SHR and lodgepole pine mortality in stands that he measured. Losses increased with increased crown competition and lodgepole pine basal area. Poor results were obtained with this system, however, when it was applied to stands in southern Montana, southeastern Idaho, and northwestern Wyoming (McGregor 1978). In these areas, infestations have been more intense in open rather than in dense stands and lodgepole pine mortality in mixed species stands has been proportionally about the same as those in pure lodgepole pine stands over a wide range in SHR.

Periodic growth ratios have been suggested as a way of evaluating stand hazard to the mountain pine beetle (Mahoney 1978). The formula for PGR is:

$$PGR = \frac{\text{Current 5-year radial increment}}{\text{Previous 5-year radial increment}}$$

PGR is considered a measure of the current trend in stand vigor. If this value is 1.0, then stand growth and vigor have been fairly stable over the past 10 years; a value greater than 1.0 indicates rising growth and vigor and less than 1.0 indicates a decline in vigor. A value of 0.9 is considered a substantial decline in vigor, which would indicate a lodgepole pine stand that will generate an increasing mountain pine beetle population and sustain an epidemic (Mahoney 1978). Good agreement was reported for PGR and beetle activity in some stands in northern Idaho and western Montana (Mahoney 1978). A problem, however, with the use of PGR is that the formula does not distinguish between fast- and slow-growing trees. For example, suppressed and dominant trees can have the same PGR, but one group obviously is in much better health and will have thicker phloem than the other.

The climatic suitability for an outbreak to occur has been combined with age and tree size for a risk rating system (Amman and others 1977). Climatic suitability is based on actual tree losses to the beetles for many combinations of elevation and latitude ranging from Colorado to the Canadian border (fig. 24). Risks have been assigned to each of three factors--climatic suitability, tree age, and tree size (table 10). By multiplying risk factors (1=low; 2=moderate; 3=high) the stand's susceptibility to beetle infestation and tree mortality is obtained (low = values 1 to 9; moderate = value 12 to 18; high = 27). One exception to these ranges occurs when all three factors are rated moderate, but the value (8) falls within the range of low risk. This is the only case where a conservative estimate of beetle potential is made when it should be higher. This system has worked well in identifying high risk stands prior to large beetle outbreaks⁵ but cannot be used in stands undergoing large outbreaks⁶ because emigrating beetles infest and kill many small diameter trees that would not usually be infested during the early part of an outbreak. The beetles do not produce much brood in such trees (Cole and Amman 1969; Amman 1969), but, nevertheless, many small trees are killed after the beetles build up in stands containing large trees.

The risk rating systems presented here were developed from unmanaged stands where ranges are large in both age and diameter. Although many factors now used probably will also prove useful to risk rate managed stands, new criteria will need to be established for defining risk classes because of the more uniform age and stand structure expected in managed stands.

⁵Gibson, K. E., and M. D. McGregor. 1979. A review of selected mountain pine beetle epidemics and the infestation potential for the Tally Lake Ranger District, Flathead National Forest, Mont. Rep. 79-5. 13 p. USDA For. Serv., Reg. 1, State and Priv. For., Missoula, Mont.

⁶McGregor, M. D., D. R. Hamel, and H. E. Meyer. 1978. Status of mountain pine beetle infestation, Bozeman-Gallatin Ranger District, Gallatin National Forest, 1977. Rep. 78-4. 11 p. USDA For. Serv., Reg. 1, State and Priv. For., Missoula, Mont.

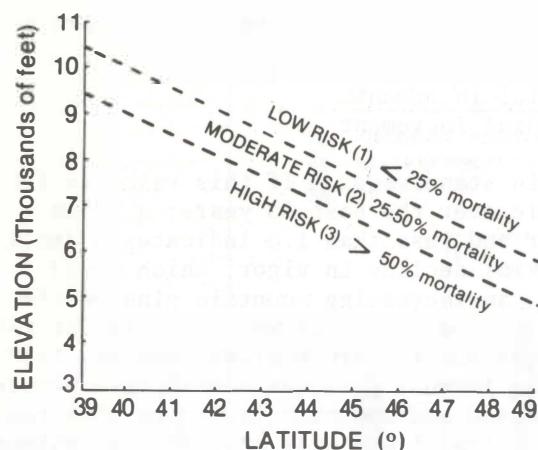


Figure 24.--Risk of mountain pine beetle infestation in lodgepole pine can be defined by zones of elevation and latitude. Percent mortality is for trees 8.5 inches (21.6 cm) d.b.h. and larger (Amman and others 1977).

Table 10.--By multiplying the following risk factors (1 = low; 2 = moderate; 3 = high) for elevation and latitude, average age, and average d.b.h., the stand's susceptibility classification is obtained; low = 1 to 9; moderate = 12 to 18; high = 27 (Amman and others 1977)

Elevation-latitude		Average age		Average d.b.h.	
		Years		Inches	
High	(1)	<60	(1)	<7	(1)
Moderate	(2)	60-80	(2)	7-8	(2)
Low	(3)	>80	(3)	>8	(3)

The risk rating systems point out characteristics that usually are found together where mountain pine beetle epidemics occur:

1. Climatic suitability of stand location.
2. Average tree diameter 8 inches (20.5 cm) or more.
3. Average age 80 years or more.
4. Twenty-five percent or more trees 8 inches (20.5 cm) or more d.b.h. with phloem thickness 0.11 inch (2.79 mm) or more.
5. And in addition to the above, high CCF and declining PGR appear to be considerations in some western Montana and northwest Idaho habitat types where lodgepole pine plays strictly a seral role in succession.

When stands have these characteristics, the land manager, if he plans to let the trees continue to grow, must monitor the stand frequently for signs of beetle activity and be prepared to harvest immediately.

None of the risk rating systems pinpoint exactly when a beetle outbreak will occur. Crookston and others (1978) use a stand growth projection model and a mountain pine beetle outbreak model to evaluate various management alternatives (Stage 1973) on subsequent beetle outbreaks and tree killing. This system, however, is applicable only to the limited geographical areas and stand situations embodied in the stand risk rating system of Schenk and others (unpublished but cited by Mahoney 1978) upon which it is based. Cole and others (1976) presented models that show how beetle production and tree losses occurred during an infestation. Losses over time generally follow this pattern. When stands adjacent to heavily infested stands are invaded by migrating beetles, however, tree losses may occur in 2 to 3 years that took 5 to 6 years in the stands where beetle outbreaks originated (McGregor 1978).

At this time we would recommend that the system of Amman and others (1977) be used to determine stand risk to beetle infestation. Diameter at breast height is usually obtained in a standard forest cruise and, because phloem and d.b.h. are usually closely related, d.b.h. can be used as an indicator of phloem thickness and beetle production. In addition, diameter also is an indirect measure of moisture content, an important factor in brood survival (Amman 1977). Large diameters maintain a higher moisture level throughout beetle development than small diameter trees, resulting in greater beetle survival. Although phloem thickness translates more directly into beetle production, presently it is a more time consuming measurement to make than d.b.h. Use of an electrical resistance meter, however, holds promise as a very rapid method of determining phloem thickness (D. M. Cole and Jensen, 1980).

MANAGEMENT ALTERNATIVES AND SILVICULTURAL PRACTICES FOR ATTAINMENT

The almost constant mountain pine beetle pressure being exerted on lodgepole pine forests poses perplexing management problems. These problems involve: (1) setting a maximum acceptable loss level; (2) determining long-term management goals to reduce losses to the beetle; and (3) making provisions for invoking emergency measures to control beetle infestations that violate the bounds allowed by items (1) and (2). Beetles disrupt sustained-yield forest regulation because of repeated depredations on mature forests. The repeated thinning from above by beetles is a silvicultural catastrophe (Wellner 1978).

One of the basic objectives in managing lodgepole pine stands is to optimize stand productivity for the particular site. Such management will involve altering stand conditions that favor the buildup of mountain pine beetle populations and to do so with full consideration of other resources and other tree mortality factors. Since the beetle is such an important factor in lodgepole pine ecosystems, many management decisions will be governed by the capability to predict beetle outbreaks, with known probability over time and a wide range of stand conditions. Consequently, there is a need to consider tree, stand, and site characteristics that affect and encourage beetle populations. Plans developed to prevent or to reduce mountain pine beetle population buildup in lodgepole pine stands must consider renewable-resource silviculture. This means that the forest is of primary concern and that such plans should deal not only with the mountain pine beetle, but with other mortality factors as well. Such factors will require appropriate modification in stand management and silvicultural practices.

Determining Acceptable Risk

Since the beetles show strong preference for large diameter lodgepole pine, the manager must decide how much risk he is willing to accept if he desires large diameters or else be willing to accept and manage for small diameter trees. If the risks of attaining large size trees are too high to accept, the manager has several other management options--type conversion, shorter rotation, species and age class mixtures.

Type Conversion

Some objectives of management can be met as well with one forest type as another. For example, a subalpine fir-Engelmann spruce or a Douglas-fir forest could serve watershed management, recreation, range, wildlife, and, in some instances, timber objectives as well as a lodgepole pine forest. The type of conversion can be accomplished naturally through culturing the understory or artificially by cutting, then planting or seeding the desired species.

Shortened Rotations

Another alternative is to select as an objective the smallest tree size that will fulfill product requirements and the shortest rotation to grow trees to this size. The size selection should be based upon the greatest beetle risk that the manager is willing to accept. Thus, he would probably select a small size objective and a short rotation for growing trees on high risk habitat types, especially at low elevations. A larger size objective could be set for low risk habitat types, particularly at high elevations. Because beetle infestations seldom occur in stands less than 60 years old (Safranyik and others 1974) a rotation of at least 60 years is probably assured.

Mixed Species Stands

A third alternative is to develop mixed stands including lodgepole pine. Beetles appear to infest mixed lodgepole pine stands as readily as pure stands (Amman and Baker 1972). In most lodgepole stands, however, some trees will survive to 16 inches (41 cm) d.b.h. even in mixtures, and other species will help to maintain higher stocking than would be the case in pure, decimated lodgepole pine stands. Overall production would be higher in mixed stands than in pure stands. Such mixed stands would meet recreational, wildlife, and watershed objectives as well or better than pure lodgepole pine forests.

Age and Species Mosaics

Achieving a desireable mix and juxtaposition of age classes (Roe and Amman 1970) and tree species (Wellner 1978) provides yet another management alternative. Breaking up a stand into several age classes and separating similar age classes with other species would probably do two things: it would eventually place the minimum area in beetle-susceptible stands, making prompt removal of these stands or the application of control measures more feasible when such stands become infested, and, it would limit the size of areas and this separation of stands might prevent large continuous infestations. The objective of creating a variety of stands, many with conditions unfavorable to beetles, can only be met through long-range planning, good markets, adequate road systems, and the passage of time. Many lodgepole pine forests are difficult at best to manage for timber products (Benson 1975; Schweitzer 1975). Generally, the small size of lodgepole, compounded with the mountain pine beetle's strong attraction to the largest diameter trees, limits opportunities for growing lodgepole pine at present. Until small trees are merchantable in lodgepole pine forests, intensive timber management will continue to be difficult (Wellner 1978).

Another Potential Alternative

Roe and Amman (1970) speculated that the faster growing genotypes may be diminishing under beetle pressure. Amman (1977), on the other hand, also speculated that the beetle may be promoting stand vigor in persistent and climax lodgepole pine stands, and thus may be partially responsible for selection of the fastest rather than slowest growing lodgepole genotypes. Because these considerations are purely theoretical, studies of genetic variability in these beetle-infested stands are urgently needed to determine the validity of either theory. If the beetle is selecting against the fastest growing genotypes, then some attempt should be made soon to preserve these genotypes.

All intermediate or harvest cuts of lodgepole pine must be considered in light of how they influence the overall compatibility of silvicultural regeneration systems, other resource values, and overall objectives of management. Consequently, managers must recognize the critical differences in prescriptions for such different situations as pure versus mixed species stands, even-aged versus uneven-aged stands, current versus future stocking, and differences in habitat types and elevations. The role of fire, diseases, and stage of succession will also influence the type of silviculture to be employed. Considering all these factors, the manager has several strategy options, depending upon whether the stand is immature or mature:

1. Restrict lodgepole pine management to the higher elevations and low risk habitat types, thus accepting slower growth and longer rotation.
2. Redistribute stand growth through repeated thinnings of immature stands to obtain large diameter lodgepole pine sooner and harvest before or upon the first signs of beetle activity. This has the highest risk factor, but recent observations suggest that cutting prior to phloem maturation or before phloem thickness exceeds critical threshold levels (about age 60 to 80 in the case of fast-growing trees) may significantly lower the risk situation for these size objectives.
3. Direct the growth and harvest of immature lodgepole pine stands to younger and smaller diameter trees than those susceptible to beetle epidemics. This will entail the silvicultural practice of stocking control.
4. Clearcut mature stands and start anew.
5. Partial cut and convert multiaged stands to younger stands. To pursue this option, the manager must consider all ramifications of the risks involved including promotion of dwarf mistletoe infection, increased windthrow, and possibly less production than with clearcuts.

Silvicultural practices to attain these management strategies are discussed in more detail in the following sections.

Stocking Control

Stocking control is probably the most important consideration in preventing mountain pine beetle epidemics in pure, even-aged lodgepole pine stands (D. M. Cole 1978). Whether one accepts high stand vigor as primary to beetle outbreaks or as a preventive to outbreaks, vigor can be more or less regulated through stocking control. Tree and hence stand growth is governed through stocking control; thus diameter, as well as phloem thickness, can be held to distributions that are not particularly favorable to mountain pine beetle epidemics.

The net response of the beetle to improved stand vigor of managed stands (age disregarded) is not yet known. We can assume for now, however, that improved vigor of trees through stocking control will have three possible results: (1) the dimensions of phloem thickness and diameter that favor beetle survival and thus encourage beetle epidemics will develop sooner; (2) younger (immature) phloem tissue, for otherwise susceptible phloem and diameter dimensions will render the stand unsusceptible until a later age; or (3) provide trees that do not favor the associated secondary bark beetles that are suspected of assisting the mountain pine beetle through its endemic state (Amman 1978). If the first is true, then reduced tree size and rotation cycles can be extended beyond those indicated by unmanaged stands. Marketability of the smaller products is the only restraining factor to the first eventuality at present, but this should decrease in importance in the future.

Repeated Thinnings

Growth is redistributed to the larger stems, but total basal area is not increased by repeated thinnings in stands that have not stagnated (D. M. Cole 1975). Although total volume production is increased by repeated thinnings in stagnated stands, the bulk of the effect is due to the initial thinning, which achieves stocking control. Repeated thinnings also tend to reduce dwarf mistletoe infections (Oscar Dooling, personal communication, May 1979). Since thick phloem is functionally related to tree vigor (D. M. Cole 1973), repeated thinnings would likely increase the probability of mountain pine beetle infestations beyond tree age 80.

Clearcutting

Clearcutting remains one of the best management techniques to convert mature stands to younger stands and create conditions favorable to regenerating lodgepole pine (Alexander 1975; Tackle 1961). Judicious and selected block or patch cutting within the extensive pure, even-aged stands of lodgepole pine can create forests with reduced potential for beetle epidemics (Roe and Amman 1970; Amman 1976). Breaking up these continuous lodgepole stands into small blocks or patches, varying in age and size classes, decreases potential for epidemics and reduces loss for any one area should an epidemic occur.

At least 15 years lead time in planning and executing block cutting to control losses due to the mountain pine beetle is recommended (D. M. Cole 1978). Most of the recent losses could have been prevented or significantly reduced had block clearcutting been planned and accomplished or at least started 20 to 35 years ago. Poor markets and economics of lodgepole pine did not encourage such action at that time, however. In addition, the mountain pine beetle-lodgepole pine interactions were not well understood. Improved markets for smaller trees and new knowledge concerning mountain pine beetle dynamics are expected to encourage planned management of lodgepole pine in the future.

Block clearcutting schedules to reduce mountain pine beetle populations should be compatible with objectives of multiple-use management and based on probability of stands sustaining epidemics. Models for predicting stand growth have been developed (Stage 1973; Myers 1971; D. M. Cole and Stage 1972) that work well for determining the effects of various management alternatives. Caution is needed, however, at this time in modifying such models to forecast the interaction of the mountain pine beetle and lodgepole pine forests over time. Without full consideration of biological principles, of logic, and of beetle behavior, erroneous conclusions can be drawn. For example, the probability of a beetle outbreak (Crookston 1978; Crookston and others 1978), coupled with the stand prognosis model (Stage 1973), is based on high crown competition factor (CCF) and high percentage of lodgepole pine basal area in the stands. The relation of beetle outbreaks to high CCF appears to occur only in parts of northern Idaho and in some stands in western Montana (Schenk and others unpublished but cited by Mahoney 1978), but not in the large block of lodgepole pine around Yellowstone Park (McGregor 1978) and on south to Colorado.

Clearcutting and regenerating the stand is probably the best way to handle stands that have a high proportion of trees that contain thick phloem, even in small diameters. For example, in the Buffalo Peak area of Colorado, clearcutting was used to prevent losses to the beetle because a high percentage of the trees, even those 8 inches (20.5 cm) d.b.h. had thick phloem (fig. 21) (Cole and Cahill 1976). Some stands in the Lazier Creek drainage on the Lolo National Forest in Montana were also clearcut; here exceptionally thick phloem occurred even in small diameter trees⁷.

Partial Cuts

Partial cuts can be used to preclude losses from impending epidemics of mountain pine beetle in special situations (Alexander 1975; Amman 1976). To address the beetle problem, overwood removal, modified shelterwood, and group selection cuttings are the only silviculturally sound forms of partial cutting available to managers where (1) multiple-use considerations preclude clearcutting, (2) combinations of cleared openings and high forest are required to meet various forest uses, and (3) regeneration of the stand is difficult after clearcutting (Alexander 1975). Partial cutting is especially attractive in cases where clearcutting is unacceptable due to visual and environmental impacts; and, regardless of the beetle, may be the cutting method of choice in two- and three-story stands if they have vigorous understories, low dwarf mistletoe infection, and low risk of windthrow. There are, however, advantages and some rather serious concerns in applying partial cuts to reduce mountain pine beetle infestations in lodgepole pine (D. M. Cole 1978). Partial cuts may leave many dwarf mistletoe-infected trees in the stand, resulting in increased infection to understory trees and overall reduced productivity of the stand (Hawsworth 1975). Windthrow is also an important consideration in some stands prone to high winds (Alexander 1975). These factors, in conjunction with current crown structure and understory situation, must be carefully considered for partial cuts to be silviculturally compatible in terms of regeneration needs, maintaining stand productivity, and meeting current and future threats from the mountain pine beetle. This compatibility is met by partial cuts in some stand prescriptions, but not others. How the factors--number of crown stories, species composition, understory condition, windfall risk, and dwarf mistletoe--determine the applicability or nonapplicability of partial cutting for a specific stand is discussed thoroughly by Alexander (1975).

Several tests of partial cuts to reduce mountain pine beetle infestations experimentally and operationally have been applied (Cahill 1978; Hamel 1978). The partial cut approach was used on over 4,000 acres (1 600 ha) in Middle Park, Colorado, to reduce losses to the beetle and avoid the visual impact of clearcuts (Cahill 1978). In addition, partial cutting was used to reduce the potential for beetle buildup in stands adjacent to clearcuts in order to avoid having extensive clearcut areas. All attacked trees and all or most of the trees 12 inches (30.5 cm) d.b.h. and larger were cut first within these stands. Then as many of the 10- and 11-inch (25.4- and 27.9-cm) d.b.h. trees as were needed were removed (regardless of vigor) to make up the remaining basal area of the cut. All trees 8 inches (20.3 cm) and larger could have been removed to further reduce susceptibility of the stand where a high percentage contained thick phloem. A second cut will be made in about 10 years.

⁷McGregor, M. D., D. R. Hamel, R. C. Lood, H. E. Meyer, and S. Kohler. 1975. Evaluation of mountain pine beetle infestations, Lazier and Meadow Creek drainages, Plains District, Lolo National Forest, Montana. Rep. 75-17. 11 p. USDA For. Serv., Reg. 1, Missoula, Mont.

A "do nothing" alternative was selected for stands too steep to log and for those that were inaccessible for other reasons. Subsequent losses to the beetles were greatly reduced in the partial cut stands. Postlogging surveys showed the trend of loss to be static to decreasing with accumulated losses of only 1 to 2 percent of the residual trees. In the "do nothing" stands, the infestation continued, and 39 percent of the trees, or 52 percent of the basal area, was lost to the beetle (Cahill 1978).

A second test of the use of partial cutting to reduce mortality was conducted in the West Yellowstone area of Montana (Hamel 1978). In this study, six 40-acre (16-ha) blocks of lodgepole pine were selected for the following harvest strategies:

1. Removal of all infested trees and all green trees 7 inches (17.8 cm) d.b.h. or greater.

2. Removal of all infested trees and all green trees 10 inches (25.5 cm) d.b.h. or greater.

3. Removal of all infested trees and all green trees 12 inches (30.5 cm) d.b.h. or greater.

4. Removal of all infested trees and all green trees with phloem thickness 0.10 inch (2.54 mm) based on an average of two samples taken at breast height from each tree.

5. No tree removal on two check blocks.

The results of the first 5 years after harvesting are very encouraging (Hamel 1978; M. D. McGregor provided data for 1978). In the 7-inch (17.8 cm) cut, harvest was completed in 1974. The following year only 0.2 trees per acre (0.49/ha) were infested. All but one tree was larger than 7 inches (17.8 cm) d.b.h.; therefore, they were missed during the harvest. In 1976, however, 2 trees per acre (4.9/ha) were infested, a build-up ratio of 1:10. In 1977, 4.3 trees per acre (10.6/ha) were infested, but this figure declined in 1978 to only 0.8 trees per acre (1.98/ha). Average diameter of attacked trees decreased from 7.2 inches (18.3 cm) to 5.6 (14.2 cm), to 6.2 inches (15.7 cm), and then to 6.6 (16.7 cm) in 1978 (table 11). Hamel predicted that the infestation within a 7-inch (17.8-cm) cut would be minimal due to the removal of the large diameter trees. This was true for the first year after harvest (1975), but infestation increased during the second and third years and declined the fourth year after the harvest. These infested trees, however, produced far fewer beetles than the number of parent beetles that attacked and killed the trees (Hamel 1978). These trees had thin phloem and they tended to dry excessively because of their small size. Immigration of beetles into the area from the adjacent uncut stands is the only explanation for the continued loss of trees within this stand. A marked decline to 0.8 infested trees per acre (1.9/ha) occurred in 1978, however, even though 21.7 newly infested trees per acre (53.6/ha) were found in adjacent uncut stands. Overall, tree losses were far less than in the untreated check areas (table 11).

Within the 10-inch (25.4 cm) diameter limit cut, the preharvest survey showed 4.2 infested trees per acre (10.4/ha). The first year following harvest, 2.0 infested trees per acre (4.9/ha) were recorded. This total represents a declining ratio of 1:0.6 from preharvest infestation. The second year, the infestation continued to decline to 1.2 trees per acre (2.9/ha). In the third year (1978), however, infested trees increased to 6 per acre (14.8/ha). As in the 7-inch (17.8-cm) cut, the number of trees from which beetles were pitched out increased from <1 percent before harvest to 21.3 and 49.5 percent of attacked trees following harvest. It is not known whether the pitchouts are related to increased vigor of residual trees or whether too few beetles were in the stands to kill all trees under attack. The expectation is for the infestation to continue at a low level for some years until the stand returns to diameter and phloem distributions that will result in increased beetle survival.

The 12-inch (30 cm) diameter limit cut was interrupted in that all infested trees were removed one year and the green component was removed the following year. Because of this interruption, 41 green trees that were originally marked for removal and 12 unmarked green trees, all greater than 12 inches (30 cm) d.b.h. were infested during the interim period. This amounted to 0.5 infested trees per acre (1.2/ha) the year after removal of infested trees was started and increased to 4.0 (9.9/ha) in 1978. Trees classed as pitchouts increased from 17 percent before harvest to 28 and finally to 46 percent after the harvest. Infestation levels within the 12-inch (30.5 cm) cut area increased to their original level within 3 years following harvest. The corresponding check block (B) had 2.9 infested trees per acre (7.2/ha) in 1978.

The cut based on phloem thickness alone was not considered a usable management alternative, but was intended to test the effect of food removal on a subsequent infestation trend, regardless of tree diameter. In the phloem-cut block, all diameters that had 0.10 inch (2.54 mm) thick phloem were cut. A postharvest survey the first year showed 11.4 infested trees per acre (28.2/ha), or an increase of 1:2.8 over the pre-harvest year. The second postharvest year saw the number of newly infested trees increase to 29.6 per acre (73.1/ha). The percent of trees pitching out beetles increased from 1 percent to 22 and 20 percent of trees attacked during the postharvest period. Hamel predicted at the beginning of the experiment that the beetles would be unable to maintain their numbers in the thin phloem of trees left in this stand. An examination showed that on the average fewer beetles emerged from infested trees than parents that killed the trees. Hence the prediction was true. The continual increase in infested trees, however, indicates a large beetle immigration from surrounding untreated stands. Consequently, the stand remained attractive to beetles even though most trees were of thin phloem. It is important to remember that some trees of large diameter but thin phloem, were left in the stand simply because the harvest strategy was to remove only trees that had thick phloem; therefore the beetles continued to be attracted to these large diameter trees. The increase in infested trees almost parallels that in the nearby untreated check block A until 1978 when there were only 8.5 infested trees per acre (21.0/ha), compared to 21.7 per acre (53.6/ha) in the check block.

Table 11.--Mountain pine beetle infested trees in study blocks, Gallatin National Forest, Montana, 1974-1977 (Hamel 1978; M.D. McGregor, USDA For. Serv., Missoula, Mont., furnished 1978 data)

Location	Mean number of successfully infested trees/acre (ha)				Mean diameter in inches (cm)				Percentage of attacked trees classed "pitchouts"			
	1975	1976	1977	1978	1975	1976	1977	1978	1975	1976	1977	1978
Hebgen Lake District												
7-inch block	0.2 (0.5)	2.0 (4.9)	4.3 (10.6)	0.8 (2.0)	7.2 (18.3)	5.6 (14.2)	6.2 (15.7)	7.1 (18.0)	<1.0	5.9	26.5	0.1
10-inch block	4.2 (10.4)	2.0 (4.9)	1.2 (3.0)	6.1 (15.1)	12.2 (31.0)	8.0 (20.3)	7.8 (19.8)	8.0 (20.3)	<1.0	21.3	49.5	0.9
Phloem block	4.1 (10.1)	8.9 (22.0)	23.6 (58.3)	8.5 (21.0)	11.3 (28.7)	9.7 (24.6)	9.2 (23.4)	7.2 (18.3)	<1.0	21.8	20.3	1.5
Check block (A)	2.8 (6.9)	8.1 (20.0)	26.8 (66.2)	21.7 (53.6)	10.5 (26.7)	9.8 (24.9)	9.9 (25.1)	9.9 (25.1)	<1.0	1.9	11.4	4.1
Gallatin District												
12-inch block	1.0 (2.5)	0.5 (1.2)	1.4 (3.5)	4.0 (9.9)	13.3 (33.8)	10.1 (25.7)	10.0 (25.4)	5.1 (13.0)	17.0	28.1	46.2	0.2
Check block (B)	40.1 (99.0)	20.7 (51.1)	3.9 (9.6)	2.9 (7.2)	8.7 (22.1)	7.5 (19.1)	7.2 (18.3)	8.5 (21.6)	48.4	35.0	62.4	6.0

In check block A, which was near the 7-inch (17.8 cm) phloem cut and 10-inch (25.4 cm) cut blocks, infested trees increased from 2.8 per acre (6.9/ha) the year harvest cuts were started to 2.8, 8.1, and 26.8 per acre (6.9, 20.0, and 66.2/ha) during the 3 years following the first harvest cut (the 7-inch cut). In 1978, however, the infestation declined to 21.7 trees per acre (53.6/ha) because a high percentage of the large diameter trees had already been killed. Pitchouts increased from 1 percent to 2 and 11 percent of attacked trees during the postharvest years. The loss was much greater and the pitchout rate much lower than in any of the cut blocks except the phloem cut block.

In check block B, the number of infested trees was 40.1 per acre (99.0/ha) the year harvest cuts were started. The number of infested trees declined to 20.7, then to 3.9, and finally to 2.9 per acre (51.1, 9.6 and 7.2/ha) during the next 3 years. This decline was due to the almost complete loss of large diameter trees in which beetle brood production is maintained. The pitchout rate was high in this check stand, ranging from 48 to 75 percent during the four postharvest years.

The results of this study further indicate the effectiveness of partial cuts keyed to susceptible diameters (with their inherent positive correlation with phloem thickness) for reducing the infestation potential of lodgepole pine stands. The fact that infestations were reduced initially in all diameter limit cuts, even the 12-inch (30.5-cm) lower limit cut, suggests that opening the stand and removing the large diameter component may be important. Reduced infestations could be due to increased vigor of trees in the stand because of the thinning or due to microenvironmental changes in temperature, light, and humidity, which the beetles tend to avoid. The first reason seems to be unlikely because lack of beetle response was almost immediate (the first year after the cut). If thinning is the cause, then stands thinned at regular intervals to maintain an environment unattractive to the beetles may permit trees to be grown to larger sizes than presently anticipated. Studies have been installed on the Shoshone National Forest, Wyoming, and the Lolo and Kootenai National Forests, Montana, to test this possibility⁸.

Salvage and sanitation cuttings can reduce total loss of wood from a utilization standpoint (D. M. Cole 1978). These methods, however, are certainly after-the-fact and cannot deter or prevent beetle outbreaks. Whereas salvage cuttings can reduce total loss of wood and sanitation cuttings can remove susceptible green trees within an infestation, both methods are dependent upon timber economics and governed by the need to protect other resources.

Do Nothing

Doing nothing to prevent or control beetle infestations on forested areas not included in the timber-growing land base, such as noncommercial forest lands, and national or state parks, has been considered a viable management option (Amman 1976; Amman and others 1977) and has long been a part of National Park management policy. This option is becoming increasingly untenable in some areas because beetles from epidemics within such forests immigrate to surrounding forests managed for timber products where they kill large numbers of trees.

⁸Cahill, Donn B., and Walter E. Cole. 1978. East Long Creek mountain pine beetle demonstration area project, Working Plan. 7 p. Shoshone National Forest, USDA For. Serv., Region 2.

McGregor, Mark D., and George R. Wilson. 1978. Hornet Hill mountain pine beetle demonstration area (now changed to Fishtrap area, Lolo National Forest). Working Plan. 10 p. USDA For. Serv., Region 1.

Insofar as esthetics are concerned, mountain pine beetle infestations may have little impact upon the viewer. Close views may be quite different, however, because of standing or fallen dead trees (Wellner 1978). This difference tends to subside with time, however, and whether such dead wood in the near view is objectionable depends simply upon the values of the beholder.

Dead timber can have an enormous impact particularly on access for recreation and for wildlife. There are also numerous related problems, such as maintenance of trails, fences, powerlines, and recreational areas from the effects of falling dead trees. In addition, fires associated with the large fuel buildup from the trees killed by mountain pine beetle and the windthrow and breakage following the infestation are very hot and destructive (Brown 1975). Consequently, because these problems are associated with doing nothing about beetle infestations, a deliberate fire management program utilizing prescribed burning may be appropriate in those lodgepole forests not used for timber products (D. M. Cole 1978; McGregor 1978).

Heinselman (1971) stated that only six fire policy options appear to be available to managers of wilderness areas, parks, and related nature reserves. Failure to consciously pursue a fire policy, Heinselman states, will still result in some combination of these options. The options are:

- (1) Attempt fire exclusion and accept the slow but pervasive changes in plant and animal communities that inevitably follow.
- (2) Allow "safe" lightning-caused fires to burn; allow also for some other wildfires that cannot be controlled, but extinguish the rest. If this option results in less than the natural fire frequency and burned area, so be it.
- (3) Allow "safe" lightning fires to burn, allow for some other wildfires that cannot be controlled, but prescribe enough additional controlled fires to assure the natural fire regime.
- (4) Suppress all wildfires to the extent feasible, and duplicate the natural fire regime with prescribed-controlled fires.
- (5) Allow all wildfires to burn unchecked unless life or property are directly threatened, and hope that a natural fire regime will result.
- (6) Abandon the ideal of natural ecosystems and turn to full-scale vegetation and environmental manipulation by mechanical and chemical means, seeding, planting, and so on. Attempt to produce desired vegetation with the tools of applied forestry.

Heinselman (1971) favored either option (3) or (4), depending on fire control, human safety, and property safety considerations of the area. Either of these options would provide approximately the natural fire regimen and avoid the risk of letting wildfires get out of hand before control is attempted.

The second option would allow for "safe" lightning fires and some escapes, but not prescribed fires, and may be acceptable where it would yield a regimen similar to that of natural fire. In isolated mountain areas, this policy may be used where little possibility exists of fires escaping to lands outside the wilderness or park.

Heinselman (1971) discounts the last option, mechanized forestry, as being inconsistent with the basic philosophy and objectives of the national park and wilderness systems.

Consequently, by utilizing fire, either prescribed or natural, mosaics of different age and size classes can be created that will mitigate the impact of mountain pine beetle infestations in noncommercial forests in a way similar to that of using mechanized forestry in commercial forests.

CHEMICAL CONTROL

Protection on a Forest Basis

Chemical control on a forest basis by spraying standing and fallen infested trees provides only a holding action at best until the potentially susceptible trees can be disposed of. A great deal of mortality results despite any immediate success of control measures. The unpredictability of these control measures and the relative certainty of reinestation of the stand leaves chemical control a precarious choice of action (Klein 1978).

Infestations of the mountain pine beetle recur rather cyclically (Roe and Amman 1970) and, as a result of these recurrences, large sums of money have been expended on attempts to control this insect. An assessment of chemical control effort against the beetle in the large outbreak on the Teton and Targhee National Forests was made by comparing stand structures from areas that were treated with chemicals on a forest basis with areas left untreated (Amman and Baker 1972). Previous efforts to evaluate control effectiveness were usually based on beetle infestation rates for short periods (a year or so) instead of stand structure during an entire infestation period (Craighead and others 1931; Miller and Keen 1960; Johnson and Schmitz⁹; Wickman and Lyon 1962).

Comparisons of lodgepole pine stand structure after infestations were completed showed that survival ranged between 62 and 90 percent of the trees 4 inches (10.2 cm) d.b.h. or larger and between 32 and 92 percent of the merchantable basal area. Survival was much greater in small than large diameter classes (fig. 25A). In six stands, mountain pine beetle infestations had ended, but had been active from 4 to 9 years. The other four stands were still infested even though outbreaks had begun 4 to 14 years earlier (table 12).

Lodgepole pine survival in the stands where infestations were completed was about the same in treated and untreated blocks within comparable elevational levels (fig. 25A). For example, the Pilgrim Mountain and Hatchet areas had similar elevations and similar tree survival. Differences in intensity and duration of infestations appear to be largely related to elevation.

⁹Johnson, Philip C., and Richard F. Schmitz. 1965. *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), a pest of western white and ponderosa pines in the Northern Rocky Mountains. A Problem Analysis, 87 p. USDA For. Serv., Intermt. For. and Range Exp. Stn., Ogden, Utah.

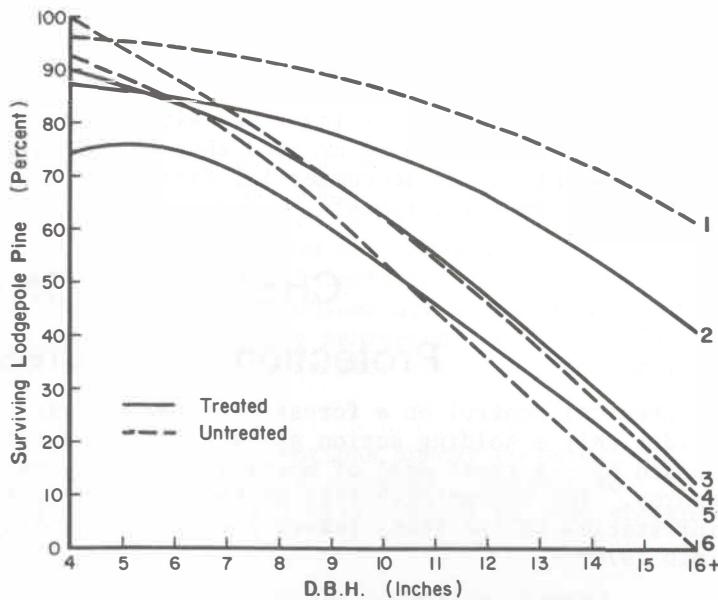


Figure 25A.--Lodgepole pine survival curves for study areas in which the mountain pine beetle infestation had ended. 1 = Togwotee Pass; 2 = Upper Spread Creek; 3 = Pilgrim Mountain; 4 = Pacific Creek; 5 = Hatchet; and 6 = Horseshoe-Packsaddle (Amman and Baker 1972).

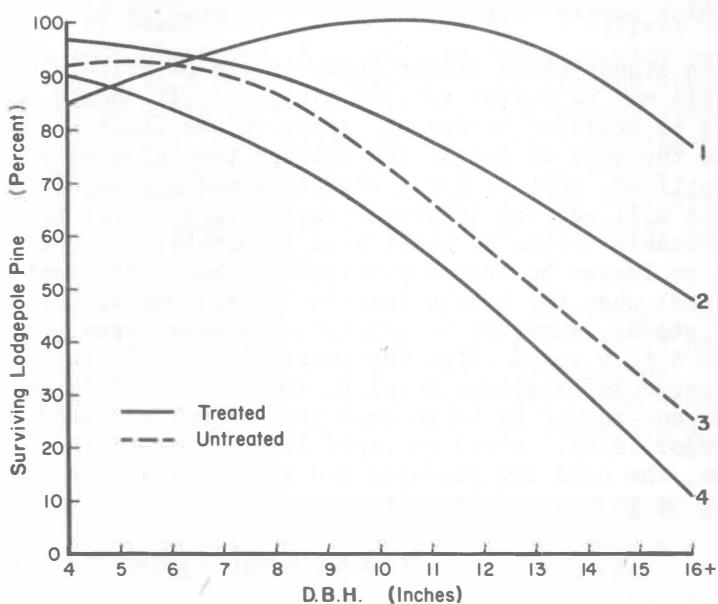
Table 12.--Periods of mountain pine beetle infestation and treatment (Amman and Baker 1972)

Block name	Years					
	Infestation			Treatment		
	Start	End	Length	Start	End	Length
Infestation concluded						
Treated						
Pilgrim Mountain	1960	1968	9	1961	1967	7
Hatchet	1960	1968	9	1962	1968	7
Upper Spread Creek	1961	1968	8	1965	1968	4
Untreated						
Pacific Creek	1961	1968	8	None	--	--
Togwotee Pass	1965	1968	4	None	--	--
Horseshoe-Packsaddle	1961	1968	8	None	--	--
Infestation continuing						
Treated						
Signal Mountain	1956	Current	14	1957	1966	10
Warm River	1965	Current	5	1966	Current	4
Pineview	1966	Current	4	1967	Current	3
Untreated						
Pine Creek	1966	Current	4	None	--	--

¹Subtle increase and decline in infestation was difficult to date. The main infestation period was 1965-1968.

The Signal Mountain area in Grand Teton National Park is of particular interest because it was still under attack after 14 years (fig. 25B). The infestation was treated during 10 of these years and the mortality rate slowed. When control efforts were discontinued, the beetle population increased. This buildup suggests that factors contributing to increases in beetle populations still existed; for example, trees of thick phloem and large diameter were present. After chemical treatment was stopped, the beetle population increased; in 1969, 24 newly infested trees per acre (59.3/ha) were recorded. Survival of lodgepole pine 4 inches (10.2 cm) d.b.h. or larger had been reduced to 76 percent and for trees 9 inches (22.9 cm) d.b.h. or larger to 46 percent--not unlike the untreated blocks. The large, then current beetle population caused additional mortality on Signal Mountain so that pine survival now is probably comparable to that in untreated areas of similar elevation.

Figure 25B.--Lodgepole pine survival curves for study areas where the mountain pine beetle infestation was current. 1 = Pineview; 2 = Warm River; 3 = Pine Creek; and 4 = Signal Mountain (Amman and Baker 1972).



Conclusions drawn from these comparisons were that control efforts did not save trees, but, in some cases, can slow and prolong the period of infestation; however, ultimate stand structure will be the same in treated and untreated stands at similar elevations.

The question arises, why are control projects ineffective? The effectiveness of a chemical control project in reducing mountain pine beetle populations and hence tree losses is related to at least seven operational factors: (1) steepness of terrain; (2) ease of access; (3) training of control personnel; (4) experience of control personnel; (5) radius of treatment application around the stand of protected trees; (6) acreage infested; and (7) initiation of control efforts while the infestation is small. In areas that had the lowest amounts of tree mortality, most of these factors were optimal.

Cost benefit ratios become an important consideration when treatment periods extend over a number of years. For example, on Signal Mountain in Grand Teton National Park, the preservation of esthetic values was of primary concern; however, in spite of 10 years of control work (1956-1966), the mountain pine beetle population increased again and, more than likely, the infestation continued until the proportional survival by diameter class was similar to that observed in untreated areas. Beetle activity continued until most trees of large diameter and thick phloem were killed. It would appear that attempts to suppress beetle populations are of little or no value in areas where timber products are not involved and that the eventual survival of lodgepole pine will be about the same whether or not the stand is chemically treated. In either case, tree cover will persist. Where lodgepole pine is persistent or climax, many of the smaller trees will survive. In such cases, openings created when overstory trees are killed will be seeded to lodgepole pine. Where lodgepole pine is seral, succeeding species such as subalpine fir and Douglas-fir will become more abundant with each mountain pine beetle infestation (Roe and Amman 1970).

In stands where timber products are of primary concern, a thorough economic analysis may be useful to land managers. It should be emphasized that protected timber should be utilized before the stand volume falls below a merchantable threshold and before the cost of protection exceeds the value of protected volume. Protection, to be justified, must be for a predetermined period of time so that the volume at time of harvest will warrant treatment expenditures. For example, if 50 percent survival of merchantable volume or basal area is arbitrarily set as the level at which a stand could no longer be logged profitably, than sufficient basal area should remain (or be retained) when the beetle infestation has ended, particularly at high elevations. In other stands, survival of merchantable basal area was reduced to less than 50 percent within 8 to 9 years after the start of the infestation (Amman and Baker 1972); however, once large infestations develop, immigration of large numbers of beetles into adjacent stands can result in 50 percent loss of merchantable basal area within 2 to 3 years (McGregor 1978). Based on rapid loss of merchantable basal area due to beetle infestation, the need for planning and accomplishing harvest prior to beetle outbreaks cannot be emphasized too strongly.

Individual Tree Protection

The zeal to use chemical sprays on vast acreages of infested trees changed abruptly after failure of such operations was demonstrated (Amman and Baker 1972). Emphasis shifted to protection of individual trees of relatively high value. Many early studies of sprays used to protect trees from mountain pine beetle attack were summarized by Lyon (1965). Recently, preventive sprays have been developed that are environmentally acceptable and registered for use in management of high value trees in campgrounds, picnic areas, visitor centers, and around permanent and summer homesites¹⁰ (Smith and others 1977).

¹⁰Gibson, K. E. 1977. Results of a pilot study to test the efficacy of three insecticides in preventing attacks by the mountain pine beetle in lodgepole pine. 7 p. USDA For. Serv., Intermt. Reg., Ogden, Utah.

Shade and esthetics can also be preserved by use of tree species other than lodgepole pine. Fir trees are now being planted in campgrounds on the Targhee National Forest where lodgepole pine mortality has necessitated removal of all overstory consisting exclusively of lodgepole pine. In many cases, removal of dead trees killed by the beetles left only tall lodgepole of small diameter. These were subject to windthrow and breakage, a danger to campers and their equipment. The decision was made to remove all lodgepole except for a few saplings and to plant additional lodgepole pine and fir trees. The planting of fir will mitigate the impact of future beetle infestations in lodgepole pine, and with the perfection of protective chemical sprays high value lodgepole can be protected against infestation.

Pheromones

Pheromones are chemical messengers or insect behavior regulators (Wood 1977) produced and used for information exchange by members of the same species. A terpene alcohol, *Trans*-verbenol, was the first such pheromone isolated from mountain pine beetles (Pitman and others 1968). It has proven to be a powerful aggregative pheromone when used in conjunction with host tree terpenes alpha-pinene or myrcene (Pitman and others 1978; Billings and others 1976). The pheromone, *exo*-brevicomin, is produced primarily by male mountain pine beetles (Pitman and others 1969) and functions to interrupt aggregation of mountain pine beetles in western white pine, thus preventing overpopulation of the tree; however, its function in lodgepole pine appears to be different than that in western white pine.

Pheromones have been used primarily in western white pine forests in attempts to protect host trees from mountain pine beetle attack. These attempts consisted of mass trapping and protection of trees by disruption of host selection and colonization (Pitman and others 1978). Although some effects of these treatments were noted, the use of pheromones in reducing losses to mountain pine beetle is not yet effective nor economical.

Pheromones were used in lodgepole pine to attract mountain pine beetles to trees of small diameter and thin phloem (Rasmussen 1972). The objective was to cause a population reduction since it is well established that mountain pine beetle brood production is low in small diameter trees (Amman 1969; Cole and Amman 1969; Reid 1963). Trees were baited with a combination of *Trans*-verbenol and alpha-pinene. The mountain pine beetle was attracted into the vicinity of the baited trees and often the first attacks took place on the baited tree; however, few baited trees were attacked heavily enough to kill them. The beetles usually switched their attack to a nearby tree of large diameter and thick phloem (Rasmussen 1972). Identification of other components of the beetle's pheromone complex appear to be needed before pheromone use in lodgepole pine forests is likely to reduce timber losses (Pitman and others 1978).

AN EXAMPLE OF MITIGATING MOUNTAIN PINE BEETLE IMPACTS

An interdisciplinary team of specialists in silviculture, soils, wildlife, fisheries, forest management, water, logging, and landscaping developed guidelines and prescribed treatments to mitigate the impact of mountain pine beetles in infested lodgepole pine stands on the Umatilla and Wallowa-Whitman National Forests in northeastern Oregon (Carter 1978). Their results are reviewed and used to illustrate the potential impacts of a mountain pine beetle outbreak on all forest resources. Recommended management alternatives also are presented.

Resources considered were timber, fisheries, wildlife, water, soils, recreation, and esthetics. The management alternatives selected as best meeting the overall management objectives were:

- A. No action.
- B. A two-phase harvest program over a 14-year period.
- C. A two-phase harvest program over a 22-year period.
- D. A three-phase harvest program over a 21-year period.

The management objectives selected to insure that all resources were adequately considered were:

1. Clean up the mess and reduce the fire hazard.
2. Mitigate adverse effects of management alternatives on soil, water, and wildlife.
3. Regenerate the timber stands as quickly as possible.
4. Utilize the wood fiber to accomplish 1, 2, and 3 above.

A 75,700 acre (30 648 ha) area referred to as Lane-Peet was selected for an intensive and initial study area by this team.

Each resource was considered in its entirety and in its interrelationship with other resources. The team reviewed the characteristics, historic involvement, future detrimental and/or beneficial effects each alternative would have on that particular resource. Then each alternative was evaluated and ranked from the most to the least desirable for each resource (table 13). Alternative D, the three-phase, 21-year harvest program, was selected. The team determined that this alternative would utilize the wood fiber, meet all three of the prescribed management objectives, and be applicable to all infested areas. A complete description of this analysis procedure can be found in the original Lane-Peet Study Report (Umatilla National Forest, Pendleton, Oreg., 1974).

Table 13.--Alternative treatment preference for different resource values (Carter 1978)

Resource	Clean up and reduce fire hazard	Mitigate effects on soil, water, wildlife	Regenerate timber stands quickly	Utilize wood to accomplish A, B, and C
	A	B	C	D
Timber	1 ⁴	1	3	2
Wildlife	1	4	3	2
Fisheries	1	4	3	2
Water	1	4	3	2
Soil	1	4	3	2
Grazing	4	1	3	2
Utilization	4	1	3	2
Recreation	4	1	3	2
Hunting	1	4	3	2
Fire	4	1	3	2
Visual	4	3	2	1

¹First preference = 1; second preference = 2; third preference = 3; last preference = 4.

Briefly the team's conclusions were:

1. Timber: Alternative D (table 13) came closest to meeting the silvicultural objectives--harvesting and prompt regeneration while meeting the guidelines for other resource objectives. With Alternative D, utilization of the volume available for harvest is about 10 percent less than with Alternative B, which maximizes utilization attempts. Regeneration processes could be lengthened over 21 years, allowing for additional discretion in choosing stands for treatment and in refining regeneration techniques. Alternative D does not best meet fiber production objectives, but it does best meet the multiple use objectives for this area.

2. Wildlife: Alternative D, the second choice, was selected over Alternative A, which has the least impact on big game habitat. Alternative D spreads timber removal over three entries rather than two and results in most diversification and maintenance of dense cover.

3. Hydrology-Fisheries: Alternative A would alter the flow regimen the least and impact water quality least because of no activity. Again, Alternative D was the second choice over B and C because higher peak flow will be kept at a minimum with less area being harvested, consequently, less bare soil will be created and more of the area will have a chance to recover before other areas are affected.

4. Soils: Again, by operating in only 30 percent, rather the 50 percent, of the area, there would be less area exposed at any one time with Alternative D. Then, too, the longer time (21 years) would give more opportunity to change and adjust procedures to reach the soils management objectives.

5. Recreation: Alternative B would result in faster rehabilitation, but Alternative D offered less evidence of man's activity in the surrounding environment because of the three-stage entry with moderate rehabilitation time.

6. Visual: Alternative D was the most desirable because the treatment would be spread out over a longer period of time, the area would return to its original condition in a moderate amount of time, and only one-third of the area would be affected at any one time.

This example represents the hard interdisciplinary thinking needed to formulate a plan that will reduce the impact on various forest resources once a mountain pine beetle outbreak starts or is imminent. Long-range planning that utilizes various silvicultural management techniques to prevent mountain pine beetle outbreaks is still the best strategy, however.

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This series of General Technical Reports represents much original research by the authors, but is also a review of published literature on the mountain pine beetle with particular reference to epidemic infestations. Part I addresses how the beetle "moves through" a lodgepole pine stand, with emphasis on relationships between the beetle and its environmental factors. Part II deals with the "inner workings" of a mountain pine beetle population, including the bionomics, mortality factors, and important entomological relationships. Part III is the model of the mountain pine beetle-lodgepole pine interaction, including display and progression of all variables studied within both beetle and tree populations.

KEYWORDS: *Dendroctonus ponderosae*, *Pinus contorta*, epidemic form, stand susceptibility, management alternatives.

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